

Decision Support Tools for Visualising Coral Reef Futures at Regional Scales

by

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Declarations

Statement of originality

This thesis contains no material that has been accepted for a degree or diploma by the University or any other institution. The work contained in this thesis, except where otherwise acknowledged, is the result of my own investigations.



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Abstract

Coral reefs provide essential ecosystem services that support the livelihoods of millions of people in coastal populations around the globe. However, human activities have severely degraded a large number of reefs worldwide, and reef ecosystem function is under continuing threat from anthropogenic impacts. Novel management approaches are required to sustain ecosystem function and there is a need for better scientific tools to inform coordinated management strategies for coral reefs over appropriate spatial and temporal scales. Simulation models are useful tools for projecting future responses of reef systems to multiple threats and can assist in evaluating the effectiveness of alternative management actions. This thesis presents a generic model framework that can be applied to tropical coral reef systems anywhere in the world. The model, CORSET (Coral Reef Scenario Evaluation Tool) uses dynamic equations to capture local-scale ecological processes on individual reefs. These reefs are connected at regional scales through ocean transport of larval propagules. CORSET is designed as a decision support tool for visualising reef futures over several decades at regional scales in the order of $10^2 - 10^3$ km.

The test case for CORSET is the Meso-American Reef system in the western Caribbean. Validation and sensitivity analysis for this test case confirms that the model is able to realistically capture regional-scale reef dynamics over time series of 30-100 years. A separate, validated version of the model for coral reefs in the Philippines region of the South China Sea – which has very different species, community structure, diversity patterns and threatening processes compared with the Meso-American system – demonstrates that CORSET is portable between dissimilar reef systems in different locations. Scenario analysis for these two reef systems demonstrates how CORSET can be applied to examine potential reef futures under alternative assumptions about future threats and management actions. Finally, CORSET is integrated with a dynamic socioeconomic model to produce a coupled biophysical-socioeconomic model system for reefs in the Mexican Caribbean. CORSET is the first regional-scale simulation model for coral reef ecosystems that has demonstrated utility for reef systems in different geographic regions. The model will be made generally available for use by researchers and decision makers through a web portal in the near future.

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Statement of co-author contributions

Chapters 1 – 5 of this thesis have been prepared as manuscripts for submission to peer-reviewed journals. In all cases the design and implementation of the research, data analysis, interpretation of results and manuscript preparation were the responsibility of the candidate but were carried out in consultation with supervisors and with input from specialist contributors. These contributions are outline for each chapter below.

Chapter 1: Prof. Craig Johnson (UTAS) and Dr. Beth Fulton (CSIRO) provided technical advice on model development. Dr. Tak Fung (Queen’s University Belfast) and Prof. Rob Seymour (University College London) provided equations for their local-scale ecological model which were modified and translated into Python by the candidate. Dr. Fung and Prof. Seymour also provided advice during the initial development of the regional-scale model introduced in Chapter 1. Dr. Ernesto Arias-González (University of Mérida) provided validation data from his group’s monitoring work in Mexico, and larval connectivity data were provided by Dr. Claire Paris and Dr. Laurent Chérubin (Rosenstiel School of Marine and Atmospheric Science, University of Miami). Contributing authors provided comments on the manuscript. *Melbourne-Thomas, J., C. R. Johnson, T. Fung, R. M. Seymour, L. M. Chérubin, J. E. Arias-González and E. A. Fulton, in press. Regional-scale scenario modeling for coral reefs: a decision support tool to inform management of a complex system. Ecological Applications doi: 10.1890/09-1564.1.*

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Glossary

The following modelling terms are used throughout the thesis and are defined here for the reader's convenience.

Agent based modelling: Simulates the actions and interactions of autonomous individuals (or agents) in an attempt to re-create and predict the behaviour of complex systems (also referred to as 'individual based modelling' by some authors).

Calibration: Is an attempt to find the best accordance between modelled and observed data by variation of some selected parameters.

Complex system: Refers to systems that are comprised of a large number of interacting components. Complex system are characterised by emergence (i.e. system-level properties that can not be predicted from the properties of individual components) as well as non-linear behaviours and self-organisation.

Connectivity: Refers to the rate of exchange of individuals between populations, driven largely by processes that influence larval dispersal. Connectivity can also refer to transport of suspended organic matter or dissolved nutrients.

Functional group: A classification of organisms based on morphological, physiological, behavioural, biochemical, or environmental responses, and/or on trophic criteria.

Instantiation: A term used to denote a particular 'instance' of a model, and/or to the procedure for creating such an instance. The instantiation procedure for models in this thesis involves parameterising biophysical processes, creating a gridded basemap which identifies the location of coral reefs, and formatting connectivity information so that it is compatible with the model framework.

Nutrification: An increase in the flux of nutrients into coastal waters (as opposed to eutrophication, which is an ecological process). Nutrients that typically enter coral reef systems are inorganic and organic forms of nitrogen and phosphorus, including nitrate, ammonium, soluble reactive phosphate, and dissolved organic complexes that can be re-mineralised into organic forms.

Scenario: A plausible story about how the future might unfold, constructed using models of real systems and information on current and past conditions.

Sedimentation: The import and deposition of suspended sediments into coastal marine systems (mostly via rivers and terrestrial runoff). In the models presented here, sedimentation is represented as the ecological effects of sediment deposition on coral growth, death and reproductive success.

Validation: A comparison between model predictions and empirical observations.

Context of the thesis

Threats to coral reef ecosystems

Coral reef ecosystem function is under severe threat from a broad range of stressors, and the call for improved approaches to managing these ecosystems has been resounding (Folke et al., 2004; Mumby and Steneck, 2008; Sale, 2008; Tupper et al., 2008; Bradbury and Seymour, 2009). Coral reefs provide critical ecosystem services to millions of people in coastal populations worldwide (Moberg and Folke, 1999; Cesar et al., 2003), but the healthy functioning of reef systems has declined significantly; the world has effectively lost nearly 20% of the original area of coral reefs and 35% are seriously threatened with loss within the next 10-40 years (Wilkinson, 2008). Large-scale declines in coral cover and increases in algal cover in the Caribbean and the Indo-Pacific since the 1970s (documented by Hughes, 1994; Gardner et al., 2003; Bruno and Selig, 2007; and Jackson, 2008) are generally attributed to the combined effects of overfishing, pollution and disturbance events including coral bleaching, disease outbreaks and damaging storms (Hughes, 1994; Aronson and Precht, 2000, 2001). These threats act at local and regional scales, and debate continues about the relative importance of impacts, particularly in relation to coral-algal phase shifts (e.g. Szmant, 2002; McManus and Polsenberg, 2004; Heck and Valentine, 2007). However, there is little doubt that cumulative stressors and disturbances pose a significant threat to reef health (Thacker et al., 2001; McClanahan et al., 2002; Burkepile and Hay, 2006).

Local- and regional-scale threats to reefs are compounded by the global-scale effects of climate change. Increasing frequency of mass coral bleaching together with reduced carbonate accretion under ocean acidification are predicted to reduce the structural integrity and diversity of reefs and to compromise the ecological function of reef systems worldwide (Hoegh-Guldberg et al., 2007; Donner et al., 2009). Furthermore, the frequency of intense hurricanes is projected to increase under anthropogenic climate change in some regions (Bender et al., 2010), which poses an additional risk to coral reefs. Strong policy decisions to address climate change need to be combined with local- and regional-scale management strategies for coral reef systems (Hughes et al., 2003; Wilkinson, 2008).

Coral reefs as complex systems

Given the numerous threats to coral reef health, there is a pressing need for robust tools that are grounded in sound science and that provide a systematic means to help prioritise management

actions and guide decision making. However, the development of such tools is a significant task given that coral reefs are complex systems with multiple components and processes acting at different scales in space and time, and that coral reef dynamics are inherently difficult to understand and predict (Hatcher, 1997; Hughes et al., 2005; Dizon and Yap, 2006). Two characteristics of complex coral reef systems that have relevance both to scientific understanding of reef dynamics and coral reef management are resilience and phase shifts. Levin and Lubchenco (2008) refer to ecological resilience as “the amount of change or disruption that is required to transform a system from being maintained by one set of mutually reinforcing processes and structures to a different set of processes and structures”. The impacts of chronic local stressors such as pollution and overfishing act to decrease the resilience of reef systems and in combination may exceed thresholds for fundamental changes in system state. Of further concern is the potential for chronic stressors to reduce the resilience of reef systems to disturbances such as hurricanes and coral bleaching events (e.g. Carilli et al., 2009a, 2010; Wooldridge and Done, 2009), and a priority for reef management is to build resilience to climate change impacts by managing chronic anthropogenic stressors at local and regional scales.

Abrupt changes between contrasting, persistent states of ecological systems are referred to as phase shifts (deYoung et al., 2008). For coral reefs, these occur as a transition from a coral-dominated to an algal-dominated state. Transitions may be continuous or discontinuous; while experimental evidence for discontinuous phase shifts is lacking (Petraitis and Dudgeon, 2004), results from modelling studies indicate that coral-dominated and algal-dominated assemblages can exist over the same range of environmental conditions (e.g. Mumby et al., 2007b). The existence of such ‘alternative stable states’ implies that the reversal of coral-algal phase shifts will require reduction of stressors beyond threshold values where the shift occurred initially (McManus and Polsenberg, 2004; Hughes et al., 2005; Mumby, 2009). Questions about reversibility are of fundamental importance in managing coral reefs, for example, what degree of restoration effort is needed to reverse phase shifts and restore reefs to a coral dominated state?, and would the effort necessary to reverse phase shifts be better spent protecting other reefs that have not yet undergone phase shifts?

Management decisions, and the effectiveness of management outcomes, ultimately depend on human behaviour and on the nature of interactions between social and ecological systems. Since both ecosystems and social systems are complex, interactions between the two are also necessarily complex, and are characterised by resilience and thresholds, feedbacks and other kinds of non-linearity (Liu et al., 2007). It is clear that an important challenge for coral reef research and management is to develop approaches that integrate the biophysical and socioeconomic components of reef systems (Clua et al., 2005; Hughes et al., 2005; Pelletier et al., 2005; Mumby and Steneck, 2008; Bradbury and Seymour, 2009; Cinner et al., 2009). This is especially true given the importance of social factors in the political process of decision making and in the implementation of management strategies.

Models as decision support tools for coral reef management

Models provide a useful means for dealing with complexity in ecological and social-ecological systems and are increasingly used as decision making tools for coral reef management. Simulation models are particularly useful for decision support because they facilitate scenario analysis. By

envisioning the likelihood of alternative futures under different management regimes, scenario analysis can help decision makers identify management approaches that will be robust across a range of potential future outcomes (Moss et al., 2010). Two key challenges in developing simulation models of complex coral reef systems are: (i) the multi-scale nature of processes that affect reef systems, and (ii) a lack of information about the interactions between biophysical and socioeconomic components. Simulation modelling for coral reef systems has a relatively long history dating back to the trophic mass-balance models of Polovina (1984), Atkinson and Grigg (1984) and Grigg et al. (1984). However, modelling studies have tended to focus on local-scale processes (e.g. McClanahan, 1992, 1995; McCook et al., 2001; Langmead and Sheppard, 2004; Mumby, 2006b; Mumby et al., 2006; Holmes and Johnstone, 2010) although Preece and Johnson (1993) and Johnson and Preece (1993) demonstrate that interactions between different ecological processes at different spatial scales can be important in models of coral communities. Models that incorporate biophysical and socioeconomic components of reef systems mostly deal with reef fisheries (Gribble, 2003; Kramer, 2007; Little et al., 2007; Shafer, 2007), although Gray et al.'s (2006) model also includes major industries such as shipping, oil and gas production and salt extraction.

Multi-scale, multi-process models can become very complicated very quickly. Fulton et al. (2003) emphasise that complicated models can be costly in terms of development and maintenance, and complicatedness introduced for the sake of completeness accomplishes nothing if the resulting model is not useful in the context it was designed for, or is too complex to be interpreted meaningfully. Model constructs that rely on a high technical skill-base for their application and interpretation may be ineffective as management tools if appropriate expertise is unavailable (Holmes and Johnstone, 2010). Desirable characteristics of models for decision support include:

- robust, testable frameworks;
- understandable inputs and components;
- portability (so that models don't have to be reformulated for different geographical locations);
- accessibility to end-users; and
- bottom-up architecture so that complex behaviours are not pre-programmed but are emergent.

These criteria are in line with the modelling strategy and framework of the Modelling & Decision Support Working Group (MDSWG, 2009) which has supported the research presented in this thesis (the MDSWG is part of the Coral Reef Targeted Research & Capacity Building for Management Program funded by the Global Environment Facility).

Approach

This thesis presents a generic, biophysical model for coral reef systems which couples dynamics from local- to regional-scales. Interactions between benthic and consumer functional groups at local scales ($10^2 - 10^3$ m) are linked across regional scales ($10^5 - 10^6$ m) by larval dispersal. The approach is bottom-up; discrete components are assembled to generate a portable framework which can be applied for reef systems in different parts the world with dissimilar spatial distributions of reefs,

oceanography and species assemblages. Model components and outputs are understandable to non-experts, but the system is able to generate complex, emergent patterns. Moreover, there is the facility to incorporate larval connectivity data from sophisticated dispersal simulations (e.g. Paris et al., 2007). The model, CORSET (Coral Reef Scenario Evaluation Tool), is equally applicable as a research tool or as a decision support tool for coral reef management.

Chapter 1 describes the components of CORSET and uses the Meso-American Reef (MAR) system as a test case. Reefs in the MAR region are subject to a broad range of stressors and disturbances, and the system is an interesting test case because of spatial gradients in human pressure which are associated with past and present patterns of coastal development in the region. The behaviour of the model is evaluated by (i) examining model outputs over long time series in the absence of stress and disturbance, and (ii) comparing simulated historical trajectories of reef community structure (based on known stressors and disturbance events) with empirical observations. CORSET is shown to be robust in predicting the structure of a healthy reef system in the absence of external forcings, and in reproducing broad-scale changes in reef state under a known history of stressors and disturbances. This chapter also addresses the role of larval connectivity in driving emergent spatial variability in community structure, and discusses the implications of this variability for reef management in the region.

Chapter 2 evaluates several aspects of model sensitivity and examines the implications of uncertainty in model formulation for the behaviour of CORSET. Analyses in this chapter examine the sensitivity of modelled coral community composition to parameter estimates and to spatio-temporal resolution. Reef state and recovery trajectories are shown to be particularly sensitive to parameters that determine coral growth and mortality rates. Variability in model outcomes depends on model formulation, in particular assumptions about the way parameters vary in space and time, and is greater at local scales than at regional scales. This has implications for uncertainty in predictions of local-scale coral reef community composition.

Chapter 3 presents the application of CORSET in scenario analysis for the MAR. Two complementary approaches to scenario analysis are used to characterise potential reef responses to the combined impacts of climate and land-use change in the Meso-American Reef region. Sedimentation and nutrification emerge as key factors in decreasing the resilience of reef systems to climate change effects. There is less variability in model outcomes at regional and subregional scales for degraded reefs exposed to high levels of stress and disturbance than for reef that are subject to lower levels of stress and disturbance. The results of this chapter emphasise the utility of a multi-scale approach in scenario analysis for coral reef systems.

The portability of the model framework is demonstrated in **Chapter 4**, which describes instantiation and validation of CORSET for the Philippines/South China Sea (PSCS) region. This region provides a useful contrast to the MAR case because it is so different in terms of key threats to reefs and in biodiversity and species composition. Scenario analysis for the PSCS region demonstrates how CORSET can be used to explore impacts and management responses for key threats to coral reef health in the Philippines, and highlights the importance of considering multiple stressors and larval connectivity in regional-scale management decisions.

Finally, **Chapter 5** demonstrates an approach to integrating biophysical and socioeconomic dynamics for coral reef systems by coupling CORSET and an agent-based socioeconomic model for

the Mexican Caribbean. This chapter documents the processes of model modification, synchronisation and the definition of information flows and feedbacks to achieve successful integration of the two model systems. A preliminary evaluation of outputs from the integrated model indicates reasonable predictions for fisheries and for ecological variables. The thesis concludes with a **Synthesis** that discusses overarching themes, evaluates the strengths and weaknesses of CORSET as a decision support tool, and indicates future directions for development and application of the model.

Chapter 1

Regional-scale scenario modelling for coral reefs: a decision support tool to inform management of a complex system

Abstract

The worldwide decline of coral reefs threatens the livelihoods of coastal communities, and puts at risk valuable ecosystem services provided by reefs. There is a pressing need for robust predictions of potential futures of coral reef and associated human systems under alternative management scenarios. Understanding and predicting the dynamics of coral reef systems at regional scales of tens to hundreds of kilometres is imperative, because reef systems are connected by physical and socioeconomic processes across regions, and often across international boundaries. We present a spatially-explicit regional-scale model of ecological dynamics for a general coral reef system. The model simulates local-scale dynamics, which are coupled across regions through larval connectivity between reefs. We validate our model using an instantiation for the Meso-American Reef system. The model realistically captures subregional- and regional-scale ecological dynamics, and responds to external forcings in the form of harvesting, pollution and physical damage (e.g. hurricanes, coral bleaching) to produce trajectories that largely fall within limits observed in the real system. Moreover, the model demonstrates emergent behaviours that have relevance for management considerations. In particular, differences in larval supply between reef localities drive emergent spatial variability in modelled reef community structure. Reef tracts for which recruitment is low are more vulnerable to natural disturbance and synergistic effects of anthropogenic stressors. Our approach provides a framework for projecting the likelihood of different reef futures at subregional to regional scales, with important applications for the management of complex coral reef systems.

1.1 Introduction

In the face of increased chronic anthropogenic stress and climate change, the rate of decline of marine ecosystem health is set to accelerate (Halpern et al., 2008). The biodiversity and functioning of coral reef systems around the globe is at particular risk (Hoegh-Guldberg et al., 2007), and the loss of ecological goods and services associated with coral reef ecosystems is likely to have serious social, economic, and cultural consequences for millions of people in coastal populations (Moberg and Folke, 1999; Cesar et al., 2003). There is a critical need to extend existing coral reef management approaches, and to adopt novel, cross-disciplinary and multi-scale methods (ITMEMS Action Statement 2006; Mumby and Steneck, 2008; Sale, 2008). Key steps towards improving coral reef management include: (i) understanding the effects of synergistic stressors and then acting to minimise multiplicative impacts; (ii) identifying reef areas that are inherently vulnerable to stress and designing management strategies that explicitly consider differences in vulnerability; and (iii) considering feedbacks between ecological and human systems. These are important considerations for building and maintaining resilience in reef systems (Nyström et al., 2008).

Models are fundamental tools in decision support (Van Kouwen et al., 2008), and stochastic simulation models are of particular value because they facilitate the projection of potential future outcomes under alternative resource management scenarios. However, modelling coral reef systems is inherently difficult given that they are complex systems with myriad processes acting across a broad range of scales in space and time (Hatcher, 1997; Dizon and Yap, 2006). In distilling this complexity to design models targeted for decision support, it is important to identify the indicators of reef state that are of most interest to reef managers. These include: hard coral and algal covers; fish biomass; biodiversity; disease prevalence; and the abundance of ‘special interest’ species such as turtles (Kramer, 2003; McField and Richards-Kramer, 2007). Projecting changes in these variables and identifying potential nonlinear responses to linear changes in disturbances and the magnitude of anthropogenic forcings informs both decision making for management as well as general understanding of coral reef dynamics.

Simulation models of coral reef ecosystems have been used to examine ecological responses to changes in the intensity and nature of fishing, grazing pressure, disturbance events (storm damage, coral bleaching and crown-of-thorns starfish outbreaks), nutrification and sedimentation (McClanahan, 1995; McCook et al., 2001; Mumby, 2006b; Mumby et al., 2006; Holmes and Johnstone, 2010). Limitations of existing models with respect to their application in decision support include: (i) they are usually designed to address research questions for reefs in particular biogeographic regions (e.g. the western Atlantic, Indo-Pacific or East Africa) and are not readily portable between reef systems (but see Holmes and Johnstone, 2010), (ii) they are not generally instantiated using base maps of the existing location and state of reefs and so cannot resolve real-life spatio-temporal dynamics; and (iii) they do not use spatially resolved information to describe larval connectivity. A noteworthy exception is Gray et al.’s (2006) hybrid model for the North-West Shelf of Western Australia, although this modelling framework was not targeted specifically for coral reef systems.

Connectivity of larvae and other suspended particles in marine systems has received significant attention in recent years (Chérubin et al., 2008; Paris and Chérubin, 2008; Jones et al., 2009), and is critically important for effective knowledge-based management and conservation. Questions regarding coral reef dynamics and management often relate to connectivity between reefs at regional

scales in the order of tens to hundreds of kilometres - for example: will fishing on one reef deplete neighbouring reefs of recruits? and will pollutant sources affect nearby and distant habitats? Here, we present a biophysical model of a coral reef system that addresses the issues of geographic portability, spatially resolved larval connectivity patterns and the need to consider processes across multiple spatial scales. The model describes dynamics of benthic (corals and algae) and consumer (fish and sea urchins) functional groups from local-scale reef patches ($500\text{ m} \times 500\text{ m}$) up to regional-scale reef tracts ($\sim 1000\text{ km}$).

Two key objectives in developing our model were: (i) to maintain an underlying model structure sufficiently generic to be portable between biogeographic regions supporting coral reefs, but which will still capture ecological dynamics of interest to coral reef management, i.e. a ‘minimum realistic’ model (*sensu* Fulton et al., 2003); and (ii) for model components and outputs to be understandable for non-experts. Our model is non-equilibrium, and emergent dynamics of interest to research and management are not hardwired into the system. The framework permits us to examine emergent behaviours at a range of spatial and temporal scales. The objective of our model in terms of management applications is to predict reef dynamics over time scales of years to decades and to identify trends that manifest at subregional to regional scales. We are not attempting to predict local-scale dynamics at particular sites (which requires the development of local models parameterised for specific sites).

We present a demonstration of our regional-scale model based on a parameterisation for the Meso-American Reef (MAR) system. The dynamic history of this region provides a broad range of questions for scenario modelling. Over the past 50 years the MAR has been subject to hurricanes, disease impacts and spatial gradients in human pressure such as the southward expansion of coastal development in the eastern Yucatan, increased tourism in Belize, and the impacts of sedimentation from coastal run-off in Honduras (Arrivillaga and Garcia, 2004). We validate the model using a dual approach; first, we examine how the model behaves over long time-series in the absence of forcings (fishing, hurricanes, disease, nutrification and sedimentation) to assess whether the emergent coral reef structures bear any resemblance to real ‘healthy’ coral reefs in the region. We then compare simulated historical trajectories of reef community structure based on known forcings with measured intermediate and end points of the system. Both the model validation process and emergent behaviours provide useful insights in terms of coral reef function and dynamics.

1.2 Methods

Our regional-scale model comprises multiple instantiations of a local-scale mean-field model of coral reef dynamics (Fung, 2009) that are connected by larval transport (Figure 1.1). The behaviour of the local model has been evaluated in detail; it realistically captures coral-macroalgal ‘phase-shift’ transitions that are characteristic of coral reefs (Knowlton, 1992; Mumby et al., 2007b). Since our regional-scale model is designed to be used in decision support applications for coral reef systems it is hereafter referred to as CORSET (Coral Reef Scenario Evaluation Tool). CORSET is implemented in the open source object-oriented Python Programming Language (Python Software Foundation, Hampton, New Hampshire, USA) version 2.5.

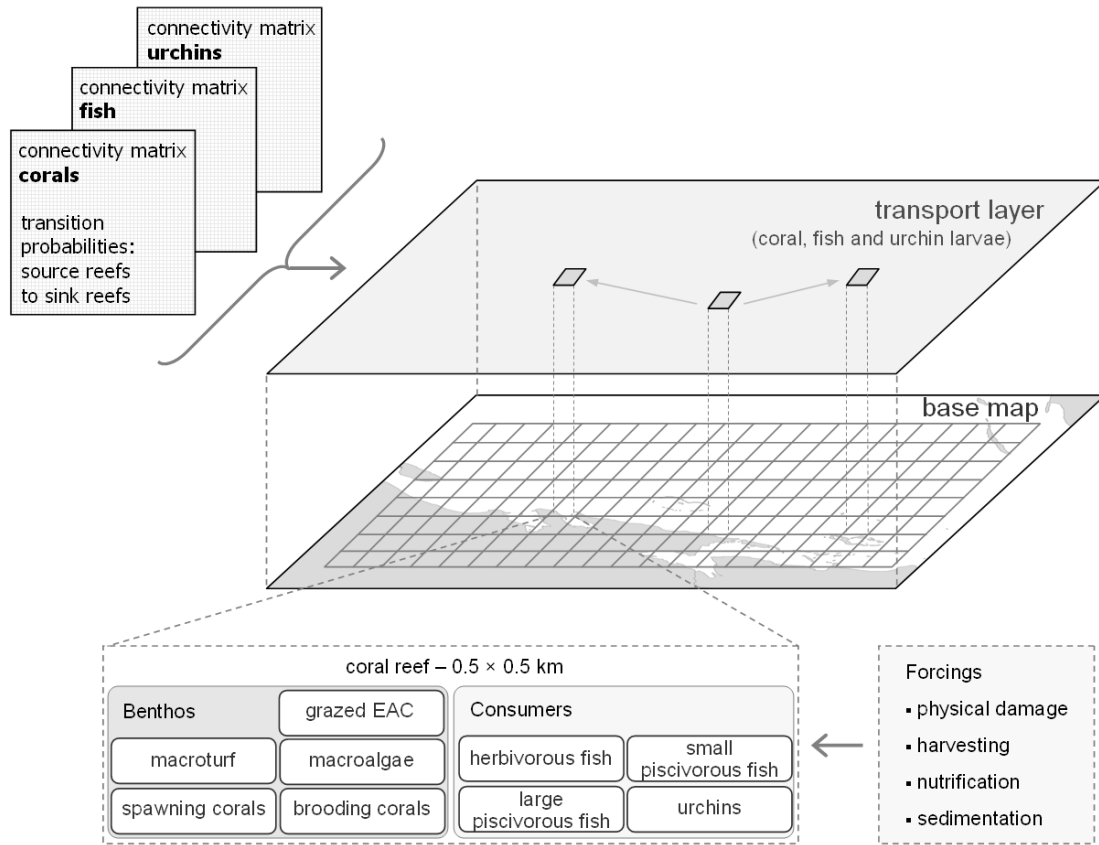


Figure 1.1: Structure of the regional model (CORSET). Eight mean-field equations describing local-scale interactions between functional groups (see Appendix A) are instantiated in each reef cell of a gridded base-map. Reef cells are connected through larval transport which is defined by connectivity matrices of transition probabilities for (spawning) coral, fish and sea urchin larvae. Fishing, pollution and disturbance are modelled as external forcings.

Model components

Local-scale dynamics in benthic cover and consumer biomass for a shallow (~ 5 m – 20 m depth) coral reef habitat are simulated using difference equations that are updated over weekly time steps. The set of equations is instantiated in each 500 m \times 500 m reef cell of a gridded base-map. Nine functional groups are modelled: brooding corals, spawning corals, macroalgae, macroalgae, grazed epilithic algal communities (EAC), herbivorous fish, small-to-intermediate piscivorous fish, large piscivorous fish and sea urchins (Table 1.1). Macroalgae refers to ungrazed algal turfs greater than ~ 2 – 4 mm in height. The grazed EAC functional group represents areas of reef that are covered by cropped algal turf (less than ~ 2 – 4 mm in height), typically growing on dead coral or non-geniculate coralline algae, that exerts a constant growth pressure, but is maintained at a low canopy height by fish and sea urchin grazing. The key functional differences between macroalgae and grazed EAC are: (i) EAC can grow into macroalgae if grazing pressure is sufficiently reduced, (ii) the recruitment rate of coral onto macroalgae is lower than the rate onto grazed EAC, and (iii)

the growth rate of coral over macroturf is lower than the growth rate over grazed EAC. Other benthic organisms such as soft corals, sponges, ascidians and clams are assumed to make non-significant contributions to the dynamics we are attempting to capture, and so are not modelled. These organisms, together with sand patches, implicitly contribute some fixed (non-dynamically variable) proportion of actual benthic space. For simplicity, and because of the spatial scale of reef cells ($500 \text{ m} \times 500 \text{ m}$), growth of benthic groups across cell boundaries and movement of fish between reef cells are not modelled. We have considered only those fish groups that are reef-associated. The three fish functional groups we model include varying proportions of commercially important species depending on the reef system to which CORSET is applied.

Table 1.1: Definitions of functional groups modelled, with example taxa for the Caribbean.

Functional group	Description
Brooding corals	Hermatypic coral species with internal brooding of planula larvae followed by release of planulae (e.g. <i>Agaricia</i> spp., <i>Porites astreoides</i>).
Spawning corals	Hermatypic coral species with broadcast spawning and external fertilization of gametes (e.g. <i>Acropora cervicornis</i> , <i>Acropora palmata</i> , <i>Montastrea annularis</i>).
Macroturf	Fast growing, filamentous algae that form patches greater than $\sim 2 - 4 \text{ mm}$ canopy height (e.g. <i>Ceramium</i> spp., <i>Enteromorpha</i> spp.).
Macroalgae	Green, red and brown algae with larger thallus size and greater structural complexity than macroturf (e.g. <i>Dictyota</i> spp., <i>Lobophora variegata</i>).
Grazed epilithic algal community (EAC)	Benthic cover characterised by non-geniculate coralline algae and dead coral skeletons. For purposes of the model, the most important feature of this functional group is that it is covered by fine algal turf less than $\sim 2 - 4 \text{ mm}$ in height. The low canopy height of this fine turf is maintained by grazing.
Herbivorous fish	Reef associated fish that feed on EAC, macroturf and macroalgae (e.g. families Acanthuridae, Scaridae).
Small-to-intermediate piscivorous fish	Fish that predate on herbivorous fish and are $< 60 \text{ cm}$ in length. Some fish in this functional group remain small-to-intermediate throughout their lifetime (e.g. some fish from families Lutjanidae, Serranidae), while a certain proportion grow into large piscivorous fish.
Large piscivorous fish	Fish that predate on herbivorous fish and small-to-intermediate piscivorous fish and are $\geq 60 \text{ cm}$ in length (e.g. fish from families Carangidae, Lutjanidae).
Sea urchins	Grazing sea urchins (e.g. <i>Diadema antillarum</i>).

Our aim in defining local-scale ecological processes was both to capture the key dynamic processes of coral reef systems, and to distil a set of interactions that are readily parameterised for reefs in different biogeographic regions. Equilibrium behaviour and parameter sensitivity of the local-scale system of equations have been examined in detail for an analogous, continuous-time (differential equations) system (Fung, 2009)*. This continuous-time system (from which our discrete-time system was derived using Euler’s method) is outlined in the Appendix A together with parameter values specific to the western Atlantic region. Where the values derived for model parameters are ranges based on empirical observations, CORSET selects values from that range at random, i.e. assuming a uniform distribution. We used uniform distributions because of a lack of information regarding the detailed shape of distributions for ecological parameters. Parameter values are randomly selected for each cell and can vary from year to year (to represent inter-annual variability in ecological processes). Those parameters that are defined as yearly rates are scaled to suit the weekly updating interval in the model.

In selecting an updating interval of one week, we faced a trade-off between model runtime and mathematical rigour. Small updating intervals reduce the number of mathematical constraints required to keep the model within the biological domain, but are associated with a nonlinear increase in computational cost. We found that CORSET behaved equivalently under weekly and daily updating intervals, but that monthly and yearly updates were associated with dynamic instability. Weekly updating confers flexibility in event scheduling, although for simplicity and consistency, the version of CORSET presented here does not include seasonality in growth processes, reproduction, recruitment, or disturbances.

Recruitment scheme

Recruitment dynamics (larval production, settlement and post-settlement mortality) are modelled explicitly in CORSET (see Appendix B), as opposed to Fung’s (2009) local-scale representation in which recruitment occurs at fixed rates. Fish and sea urchin recruits are subject to density dependent post-settlement mortality above a pre-defined threshold of recruit density (Jones, 1990), and fish recruits suffer additional post-settlement mortality in reef cells with low coral cover (Feary et al., 2007; Holbrook et al., 2008). Because published values for larval production by corals, fish and sea urchins are uncertain and variable, CORSET is tuned by varying larval production parameters within acceptable ranges derived from the literature (see Appendix B).

Larval transport is defined by transition probabilities in the form of connectivity matrices. For the MAR system instantiation of CORSET presented here, connectivity matrices for fish, spawned coral and sea urchin larvae are derived from Lagrangian Stochastic Models that incorporate physical (eddy perturbation and diffusion) and biological (vertical movement and mortality) processes (Paris et al., 2007). Connectivity matrices can be generated using proxies such as drifter data for reef systems where sophisticated connectivity information is lacking. However, there is strong evidence that over-simplified representations of larval transport, in particular the representation of larvae as neutrally buoyant particles, typically leads to overestimates of transport distances (Cowen et al., 2000, 2006). Given progress with several global ocean circulation models (e.g. Smedstad et al., 2003; Weijer et al., 2003; Chassignet et al., 2007; Oke et al., 2008), we envisage that highly

*Fung (2009) is available by email request to the author (tfung01@qub.ac.uk)

resolved hydrodynamic simulations coupled with particle tracking models, which provide connectivity estimates as output, will soon be available for most, if not all, coral reef regions of the world.

Dispersal of larvae in the MAR region was simulated using linked hydrodynamic and particle tracking modules (Chérubin et al., 2008; Paris and Chérubin, 2008). The grid resolution for hydrodynamic data, generated with the 3-dimensional Regional Ocean Modeling System (ROMS), was 2 km. Particle tracking was conducted separately for ‘generalised’ reef fish larvae, spawned coral larvae, and sea urchin larvae considering the biological characteristics specific to these groups (Table 1.2). We defined a ‘generalised’ fish larva to represent both herbivorous and piscivorous fish larvae. As in Paris et al. (2007), we applied a 9 km sensory buffer zone for larval fish denoting their ability to sense and swim towards settlement habitat on reefs (Fisher et al., 2000; Simpson et al., 2005; Gerlach et al., 2007). Fish larvae were also able to migrate vertically from the surface to deeper layers once they reached an age of 30 days, with vertical probability distributions for larvae based on field observations (see Paris et al., 2007). Larval mortality for all groups was included in the particle tracking scheme as a constant process assigned stochastically among larvae in a particular simulation. The larval transport simulations we conducted to inform CORSET provided a unique opportunity to explore differences in patterns of connectivity between functional groups in a coral reef system. Furthermore, we were able to evaluate potential ecosystem level consequences of these connectivity patterns.

Connectivity matrices for the MAR define transition probabilities between 152 reef polygon ‘nodes’ (source and settlement reefs), with average dimensions of 5 km \times 10 km (Figure 1.2B). 143 of these polygons contain reef cells at the 500 m \times 500 m resolution. It was necessary to eliminate 30 polygons as source nodes because of an artefact of domain truncation at the northern boundary of the modelled system; eliminated source nodes acted as sinks nodes only. Mapping of the 500 m \times 500 m reef cells to polygons was used to accumulate larvae at source nodes, and to distribute larvae evenly between cells within sink nodes. Brooded coral larvae are assumed to settle within natal reef polygons given short average dispersal periods for the larvae of coral species in this group (in the order of 4 days; Fadlallah, 1983).

Table 1.2: Biological parameters used for larval dispersal simulations.

	Coral larvae (spawning species)	Fish larvae	Urchin larvae
Pre-competency (days)	5 ⁽²⁾	15 ⁽⁶⁾	30 ⁽¹²⁾
Maximum competency (days)	30 ⁽³⁾	40 ⁽⁷⁾	65 ⁽¹³⁾
Mortality (day ⁻¹)	0.25 ⁽⁴⁾	0.1 ⁽⁸⁾	0.2 ⁽¹⁴⁾
Spawning season (Caribbean)	August ⁽⁵⁾	May ⁽⁹⁾	June ⁽¹⁵⁾
Vertical migration	-	after 30 days ⁽¹⁰⁾	-
Sensory zone ⁽¹⁾	-	~9 km ⁽¹¹⁾	-

Derivation details: ⁽¹⁾Sensory zone defines the distance within which larvae can detect, and begin moving towards, settlement reefs.

⁽²⁾From Baums et al. (2006) and Hughes et al. (2002), the pre-competency period for spawned coral larvae is in the range 3 – 7 days. The median period of 5 days was used in larval dispersal simulations for CORSET.

⁽³⁾Baums et al. (2006) and Richmond and Hunter (1990) describe the maximum competency period for spawned coral larvae as one month (30 days).

⁽⁴⁾The mortality rate for spawned coral larvae used by Blanco-Martin (2006) in his larval dispersal modelling study is 25% per day.

⁽⁵⁾Based on the spawning season for *Acropora palmata* (Baums et al., 2006) and *Agaricia spp.* (Mumby et al., 2007a) in the Caribbean.

⁽⁶⁾As in Paris et al. (2005).

⁽⁷⁾Victor (1991) reports that the majority of reef fishes have a pelagic larval dispersal period of 20 – 30 days. Paris et al. (2005) and Paris et al. (2007) use a 30-day competency period for modelling damselfish and snapper larval dispersal. However, Mumby et al. (2007a) use an 80-day pelagic larval dispersal period in their model for parrotfishes. Therefore, the maximum competency for generalised fish larvae in CORSET is extended to 40 days to allow for extended pelagic dispersal in some tropical reef fish (e.g. parrotfishes, chaetodontids and some wrasses).

⁽⁸⁾Based on mortality rates used by Paris et al. (2007).

⁽⁹⁾Modelling studies by Cowen et al. (2000) and Paris et al. (2007) for coral reef fish in the Caribbean assume spawning during May.

⁽¹⁰⁾As in Paris et al. (2007).

⁽¹¹⁾As in Cowen et al. (2006).

⁽¹²⁾From Eckert (1998).

⁽¹³⁾Karlson and Levitan (1990) use a 50 – 90 day pelagic larval dispersal period for *Diadema antillarum*, and Morgan and Shepherd (2006) report 2 – 19 week planktonic larval durations for urchins. Given the constraints of modelling very long larval dispersal periods (using particle tracking models), the maximum competency period for urchins is truncated to 60 days for the regional model.

⁽¹⁴⁾No data available; mortality for urchin larvae is assumed to be intermediate between that for fish larvae and coral larvae.

⁽¹⁵⁾Published studies of spawning in *Diadema antillarum* suggest there are two peaks in gonad development and subsequent gamete release in the Northern Hemisphere (in early summer and early winter; Iliffe and Pearse, 1982; Hernandez et al., 2006). For the purpose of modelling urchin larval dispersal, only the first peak was used.

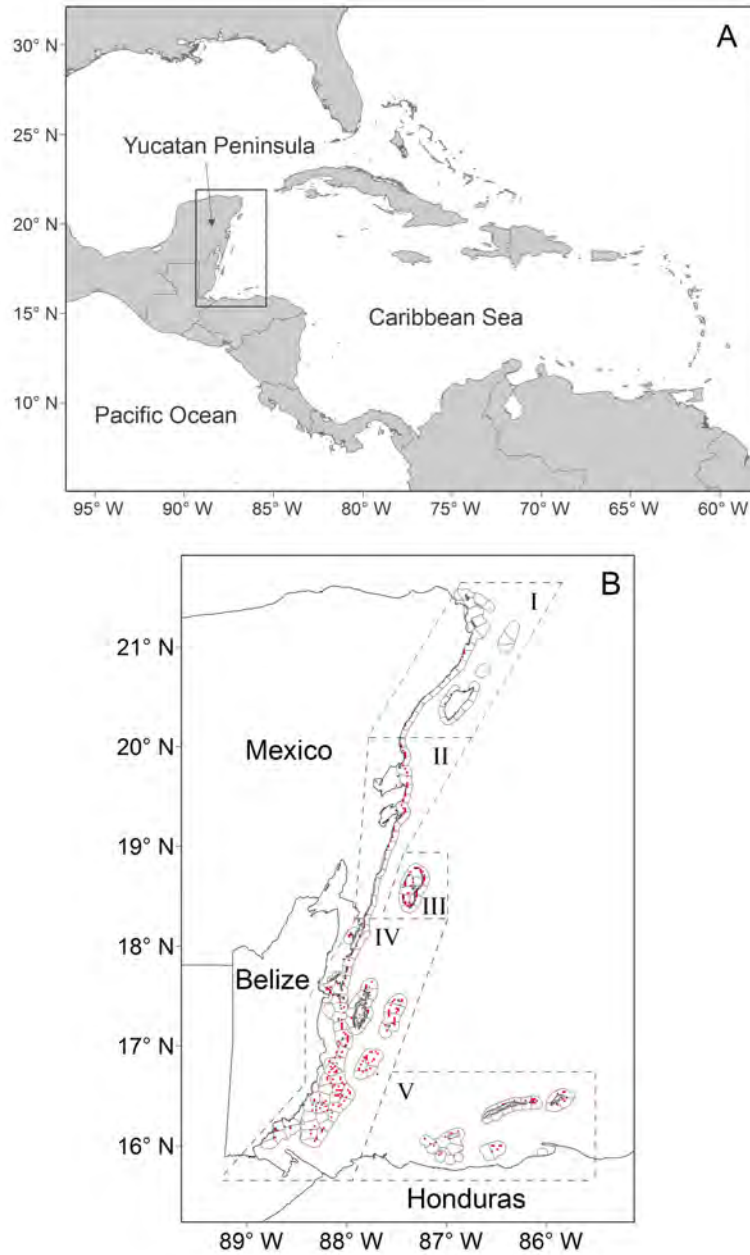


Figure 1.2: Spatial extent of the region modelled for the Meso-American Reef system instantiation of CORSET. 143 polygons used to define larval sources and sinks enclose 5368 500 m × 500 m reef cells (indicated in red). Reef cell locations were extracted from reef distribution maps from the University of South Florida's Institute for Marine Remote Sensing Millennium Coral Reef Mapping Project (IMaRS, 2004). Areas delineated by dashed lines indicate the extent of the five subregions; I, II, III, IV & V.

Forcing scheme

We use the term forcings to refer to modelled changes in fishing pressure, hurricane events, disease and bleaching events, nutrification (*sensu* Szmant, 2002) and sedimentation. The scheduling of forcings in CORSET is flexible. For example, hurricanes can be modelled with a defined long-term frequency, but where year-to-year occurrence and category strength are random. Alternatively, hurricanes can be scheduled to occur in particular years with predefined category strengths, and to affect particular subregions of the model domain. Here, hurricanes refer to tropical cyclones with maximum sustained wind speeds of ≥ 33 m/s (Nyberg et al., 2007). Hurricane forcings are modelled as a loss of coral and algal cover (Table 1.3). Based on Gardner et al.'s (2005) definitions for zones of influence for hurricanes, high category hurricanes affect a greater proportion of reef cells than low category hurricanes. Category 4 and 5 hurricanes are assumed to affect all cells within a reef tract (or subregion), category 3 hurricanes affect two thirds of cells, and category 1 and 2 hurricanes affect one third of reef cells.

As for hurricanes, disease and bleaching events in CORSET can be set to occur randomly or, in recreating known events, be scheduled to affect particular reef cells at predefined time steps. Coral bleaching and disease forcings invoke a loss of coral cover, while disease in sea urchins results in a decrease in sea urchin biomass. Fishing pressure can be scheduled to increase or decrease over time in a given model run in particular cells or subregions of the model domain. Total fishing pressure (f) is apportioned between herbivorous, small-to-intermediate piscivorous and large piscivorous fish (see Appendix A).

Nutrification and sedimentation forcings are modelled by scaling ecological processes at the local scale (Table 1.3). In reef cells affected by nutrification, the growth rate of macroalgae increases and coral larval production decreases. In sedimentation affected cells, coral growth and the survival of coral recruits decrease while coral mortality rate increases. Reef cells affected by these parameter forcings can be identified in association with nutrient and/or sediment point sources, or alternatively the proportion of nutrification/sedimentation affected cells can increase or decrease over time for a given model run. The model framework provides the capability to include sediment transport by ocean currents, however sediment transport has not been included in model runs presented here. CORSET does not currently model seasonality in forcings; fishing, nutrification and sedimentation forcings act year round, while hurricanes and bleaching/disease events occur mid-year.

Meso-American Reef (MAR) system instantiation

The spatial extent of this instantiation was $326 \text{ km} \times 632 \text{ km}$ and a total reef area of 1342 km^2 was modelled ($5368 \text{ } 500 \text{ m} \times 500 \text{ m}$ reef cells – Figure 1.2). Here, reef area refers to generic coral reef habitat (in the approximate depth range 5 – 20 m); the model does not resolve the variability or distribution of different coral reef habitat types within the MAR since our intention is to make broad predictions at regional and sub-regional scales (and not to predict local-scale dynamics). Reef locations in the MAR region are derived from The Millennium Coral Reef Mapping Project's geomorphologic classification of coral reefs (from 30 m Landsat imagery; IMaRS, 2004), and include only those classifications with a high probability of being living coral (forereef, reef flat, barrier reef

pinnacle and shallow terrace, as in Burke et al., 2004). CORSET assumes that all reef locations in the model domain can support coral cover, and that a given reef community will respond in a broadly similar way to a given major forcing.

To facilitate implementation of forcing schedules, the region was divided into five subregions following Kramer and Kramer’s (2002) Ecoregional Planning Scheme for the MAR. To validate this instantiation we present model output under two forcing schemes or scenarios. In the first, with all forcings switched off, we assess whether the model is able to produce stable long term dynamics in which reefs are recognizable as being in a ‘healthy’ state. In the second we use predefined schedules for fishing, hurricanes, disease, bleaching, nutrification and sedimentation that mimic the known sequence, location and magnitude of these events. The intention is to assess the capacity to predict the known structure of particular reef areas from a known history of forcings.

Table 1.3: The effects of hurricane, nutrification and sedimentation forcings on ecological processes in CORSET.

Parameter	Derived value(s)
Factor by which coral cover is reduced by a hurricane disturbance.	$0.002 - 0.7^{(1)}$
Factor by which macroalgal cover is reduced by a hurricane disturbance.	$0.9^{(2)}$
Scaling factor for the growth rate of macroalgae under nutrification.	$2 - 7^{(3)}$
Scaling factor for coral larval production under nutrification.	$0.75 - 1.0^{(4)}$
Scaling factor for coral growth rate under sedimentation.	$0.7^{(5)}$
Increase in coral mortality rate (per year) under sedimentation.	$0 - 0.2^{(6)}$
Scaling factor for the survival of coral recruits under sedimentation.	$0.4^{(7)}$
Recruitment rate of coral onto macro turf under sedimentation.	$0^{(8)}$

Derivation details: ⁽¹⁾Combined estimates from Bythell et al. (1993), Cheal et al. (2002), Lirman (2003), Gardner et al. (2005) and Wantiez et al. (2006).

⁽²⁾Following Mumby et al.’s (2006) model for a Caribbean forereef, it is assumed that a hurricane reduces macroalgal cover to 10% of its cover before the hurricane.

⁽³⁾The nutrification response of algae in the regional model is based on the linear threshold model described by Bell et al. (2007). The concentration of N and P combined is assumed to be above the threshold for an algal growth response in nutrient-affected reef cells. Macroalgal growth rate in these cells is scaled by the ratio of maximum growth rate to average growth rate from published values for a range of tropical algal species (Lapointe, 1989; Lapointe and O’Connell, 1989; Larned and Stimson, 1996; Larned, 1998; Schaffelke and Klumpp, 1998).

⁽⁴⁾Loya et al. (2004) recorded a 25% decrease in larval production by the brooding coral *Stylophora pistillata* under elevated nutrient conditions. Ward and Harrison (2000) report that *Acropora longicyathus* and *Acropora aspersa* (both broadcast spawners) exposed to elevated nitrogen produced significantly smaller and fewer eggs than those which were not exposed to nitrogen. The scaling factor for coral larval production under nutrification is taken to be in the range 0.75 – 1.0.

⁽⁵⁾Data from and Cortes and Risk (1985) indicate that the growth rate of *Montastrea annularis* subject to sedimentation is ~ 70% of growth rates at control sites.

⁽⁶⁾Average mortality rates reported by Nugues and Roberts (2003) for sedimentation rates in the range 1 – 12 mg cm⁻² d⁻¹ are in the order of 1.5 – 2% yr⁻¹ (as a percentage of initial surface area of tissue) for the two coral species *Colpophyllia natans* and *Siderastrea siderea*. The coral mortality rate in the regional model is assumed to increase by between 0 – 0.2 yr⁻¹ in sediment-affected reef cells.

⁽⁷⁾Babcock and Smith (2000) report that the number of juvenile *Acropora millepora* colonies surviving at sediment treated sites after 8 months was approximately 40% of levels at reference sites.

⁽⁸⁾Birrell et al. (2005) report *Acropora millepora* recruitment to sediment-treated turf algae as uniformly zero.

To test whether CORSET could capture dynamics typical of a ‘healthy’ reef in the MAR we compared mean trajectories from five runs of the model (in the absence of all forcings) with indicator values from the Healthy Reefs Initiative (HRI, 2008) Reef Health Index for the Meso-American region. Five model runs were taken as sufficient because variability in model output between runs was small (due to the parameter selection method described above). Recent observations of reef state in the MAR were used as initial conditions for this ‘healthy reef’ scenario (García-Salgado et al., 2006). We then simulated historical trajectories based on schedules of known and estimated past forcings for the MAR from 1980 – present (Table 1.4) and compared these trajectories with observations of benthic cover and consumer biomass values from ecological surveys in the region (Arias-González, 1998; UNESCO, 1998; Almada-Villela et al., 2002; Steneck and Lang, 2003; Roy, 2004; García-Salgado et al., 2006; Newman et al., 2006; Brown-Saracino et al., 2007; Marks and Lang, 2007; McField et al., 2008, Arias-González unpublished data). We assumed nominal human impact to reefs in the MAR prior to 1980 and initial conditions for historical trajectories were set within the range for healthy MAR reefs (HRI, 2008) in the absence of other information. The increase in coastal development in Meso-America over the past 30 years was modelled as a progressive increase in the number of reef cells affected by nutrification and sedimentation forcings across the entire region. Given evidence that dissolved nutrients and sediments can be transported significant distances from land-based sources (Andréfouët et al., 2002; Devlin and Brodie, 2005; Chérubin et al., 2008; Paris and Chérubin, 2008) we assumed that these forcings affected offshore atolls as well as reefs adjacent to the coast.

Table 1.4: Chronology of modelled forcings for the Meso-American Reef system, for the period 1980 – present. Spatial delineations for Subregions I – V are indicated in Figure 1.2B. Hurricane categories (at the time they intersected reefs in the MAR) were derived from NOAA National Hurricane Center (NHC) archives.

Year(s)	Subregions affected	Forcing
1980 – 2007	Entire region	Increasing fishing pressure and nutrient/sediment inputs from coastal development. ^(1, 2, 3)
1983 – 1984	Entire region	Urchin mortality event. ⁽⁴⁾
1986 – 1990	IV	Decline in coral cover due to white-band disease. ⁽⁵⁾
1988	I	Hurricane Gilbert (category 5).
1998	I, II, III & V	Coral bleaching event. ^(3, 6)
1998	IV & V	Hurricane Mitch (category 5).
2000	IV	Hurricane Keith (category 3).
2001	IV & V	Hurricane Iris (category 4).
2002	I	Hurricane Isidore (category 3).
2005	I	Hurricanes Wilma and Emily (category 4).
2007	II & III	Hurricane Dean (category 4).

Sources: ⁽¹⁾Koslow et al. (1994), ⁽²⁾Arrivillaga and Garcia (2004), ⁽³⁾McField et al. (2008), ⁽⁴⁾Lessios (1988), ⁽⁵⁾Aronson and Precht (2001), ⁽⁶⁾Steneck and Lang (2003).

Data for historical fishing pressure on functional groups of fish modelled in CORSET is lacking. Reports indicate that there has been a steady increase in fishing pressure in the MAR region since 1980, and that large piscivores have been preferentially targeted (Koslow et al., 1994; Harborne et al., 2001; Arrivillaga and Garcia, 2004). This increase was represented in our historical scenario as a progressive increase in total fishing pressure from 10% to 100% of the most recent available estimates of fishing pressure for the region (Koslow et al., 1994; Arias-González et al., 2004) over 30 years. We did not consider differences in fishing pressure between reserve and non-reserve areas as our aim was to examine broad trends in model trajectories. Note however that it would be straightforward to use our model to examine more detailed scenarios of marine protected area placement.

We modelled the 1983 – 1984 Caribbean-wide sea urchin mortality event as a 90% reduction in urchin biomass (Lessios, 1988), and the decline in coral cover between 1986 – 1990 on the Belize Barrier Reef (subregion IV) – which is presumed to have been due to mortality caused by white-band disease (Aronson and Precht, 2001) – as a 20% reduction in coral cover. The 1995 Caribbean coral bleaching event was not included in the historical scenario since this event caused minimal coral mortality in the MAR; corals recovered despite widespread bleaching (Koltes et al., 1998). We modelled the 1998 bleaching event as 20% overall coral mortality in subregions I, II, III and V, and 50% mortality in subregion IV, based on reported levels of mortality following the event (Steneck and Lang, 2003; McField et al., 2008).

1.3 Results

‘Healthy reef’ scenario

Model trajectories for benthic and consumer functional groups were stable over long time series (100 years) in the absence of stressors and disturbances (Figure 1.3), and the system can be assumed to have converged to (quasi) equilibrium. Average values across the region at equilibrium approximate indicators for reefs of ‘Good’ to ‘Very Good’ health in the MAR (HRI 2008), i.e. $\geq 20\%$ coral cover ($\geq 40\% = \text{‘Very Good’}$) and $\geq 36 \text{ g/m}^2$ herbivorous fish biomass ($\geq 48 \text{ g/m}^2 = \text{‘Very Good’}$). While predicted herbivorous fish biomass was slightly lower than expected, there is still sufficient grazing pressure to constrain algal overgrowth of coral. We tested ‘healthy reef’ scenarios with low frequency hurricanes (once every 20 years and once every 10 years), and found that these also give stable regional average coral covers $\approx 40\%$.

Empirical indicators are not available for algal cover, piscivorous fish biomass, or sea urchin biomass, however data for 11 survey sites in Belize (Brown-Saracino et al., 2007) indicates that at reef locations with high mean coral cover ($\geq 40\%$), mean macroturf and macroalgal covers were 50 – 80% and 8 – 15% respectively. Modelled values for algal cover (Figure 1.3A) were at the low end of these ranges. The maximum reported value for piscivorous fish biomass in the region, 39 g/m^2 (Arias-González, 1998), is assumed to be representative of a healthy reef state and is similar to modelled biomasses for this functional group. Values for sea urchin biomass reported by Brown-Saracino et al. (2007) are in the range $36 - 258 \text{ g/m}^2$, mostly comprising *Echinometra* spp. However, these values are much higher than biomass estimates reported by Newman et al. (2006) for the MAR ($10 - 40 \text{ g/m}^2$) who found *Diadema antillarum* to be the dominant sea urchin species.

Our simulated estimates for sea urchin biomass (Figure 1.3B) were closer to values reported by Newman et al. (2006). We note that since there is some competition for algal resources between herbivorous fish and sea urchins in the model (based on evidence from Hay, 1984 and Carpenter, 1990), we expect that at high herbivore biomass and low algal cover, sea urchin populations will be relatively low.

There was pronounced, emergent spatial variation in benthic cover and consumer biomass across the modelled region, with variability arising both within and between subregions (Figures 1.4 and 1.5). This variability was driven primarily by differences in self-recruitment and external larval supply among reefs and is emergent because of the complex nature of recruitment in CORSET. With over 12×10^3 possible larval connections between reefs for each of the three dispersed groups (spawning corals, fish and urchins), and the potential for cascading downstream effects of low or high recruitment (e.g. low recruitment to a particular reef cell will lead to reduced larval output, which will then have consequences for downstream reef dynamics, and so on), the nature of spatial variability cannot be anticipated from model inputs. The model predicted macroalgal cover to be close to zero in Belize (model subregion IV) compared with $\sim 10\%$ average macroalgal cover in other subregions (Figure 1.4A). Also emergent from CORSET was a spatially variable ratio of brooding to spawning corals (Figure 1.4B). Due to the structure of the model, brooding corals will be more successful in reef areas to which the supply of spawning coral larvae is low. CORSET predicted this to be the case for the offshore atoll Banco Chinchorro (subregion III), where arrival rates for larvae from spawning corals were only 30% of average rates for the entire MAR region. From connectivity matrices for the MAR, we identified northern Belize and Honduras (subregions IV and V) as the primary source reefs for exogenous supply of coral larvae to Banco Chinchorro.

Average piscivorous fish biomass was notably higher in Belize than in other subregions, whereas total fish biomass was low at Banco Chinchorro (Figure 1.4C). Larval dispersal simulations predicted low settlement rates of fish larvae on Chinchorro; total settlement for this subregion was only 10% of mean values for the MAR region and Honduras was the predominant exogenous source of fish larvae. The reported abundance of piscivorous fish families at Chinchorro is low, a fact generally attributed to overfishing (Loreto et al., 2003). While our result suggests that there may be other ecological factors at play – namely limited larval supply – CORSET considers only reef associated piscivorous fish species. Visitations of pelagic predators may have been frequent at Chinchorro in a pristine state.

Patterns of larval connectivity in the MAR were markedly different between functional groups (Figure 1.6). These patterns are the complex outcomes of oceanographic processes and the behavioural characteristics of the larvae themselves. In larval dispersal simulations, sea urchin larvae could spend up to 65 days in the water column and were not competent to settle for the first 30 days of this period (Table 1.2). This resulted in patchily concentrated arrival of sea urchin recruits to sink locations (Figure 1.6C) which is reflected as hotspots of modelled adult biomass (Figure 1.5C). In contrast to sea urchin larvae, simulations indicated strong self recruitment for fish larvae (Figure 1.6B – upwards diagonal of matrix), an observation that is increasingly common from field studies and modelling approaches that consider behavioural characteristics of fish larvae (Wolanski et al., 1997; Jones et al., 2005; Cowen et al., 2006). The strength of self recruitment for coral larvae was intermediate between that of fish and sea urchins. Predicted larval supply to the northern part of the MAR was depauperate for both corals and fish; sensitivity analyses

indicated that this feature is not an artefact of the elimination of some Mexican reefs as larval sources (as described in the Methods). Comparison of the modelled recruitment ratio for brooding to spawning corals with published values for the Caribbean region indicated that the modelled ratio was within the expected range. The mean ratio for the Caribbean ranges from 3 – 46 for new recruits (Smith, 1992; Langmead and Sheppard, 2004), while the ratio from CORSET is between 7 – 20.

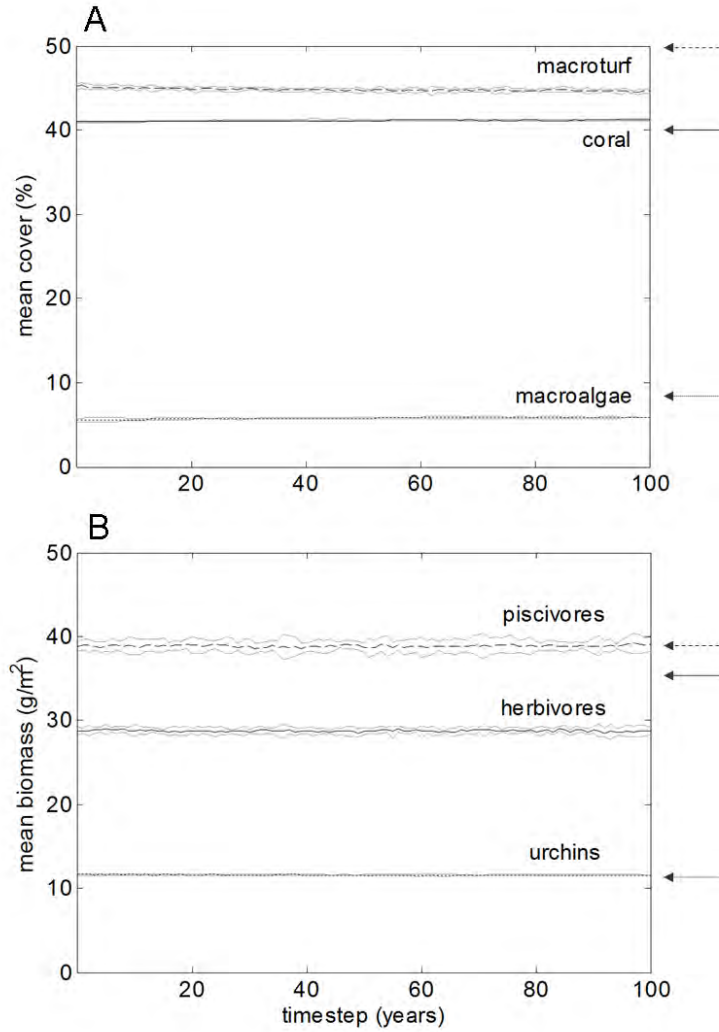


Figure 1.3: Model trajectories for benthic (A) and consumer (B) functional groups over 100 years in the absence of forcings (the ‘healthy reef’ scenario). Mean values and 95% confidence intervals from five model runs are presented (confidence intervals indicate variability between runs rather than spatial variability across the region). Equilibration time-steps (from initial conditions to quasi-equilibrium) are not shown. Values for piscivores are the sum of model outputs for small-to-intermediate and large piscivorous fish. Arrows indicate expected values for healthy reefs in the MAR.

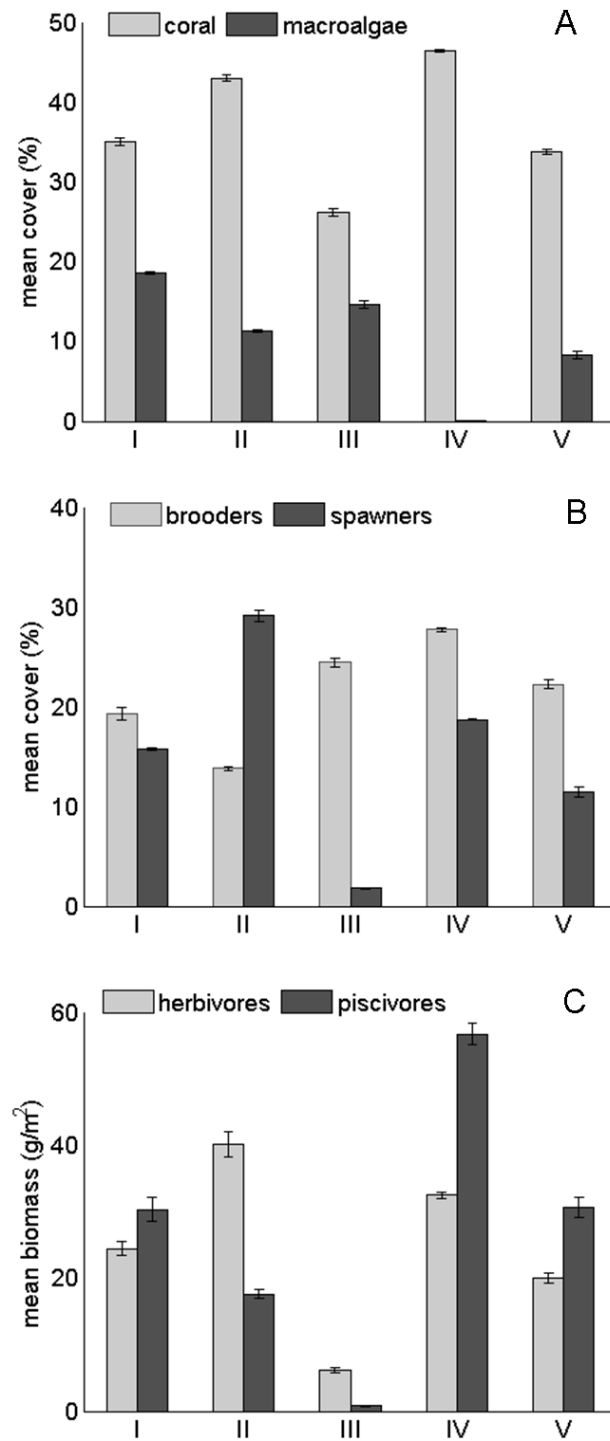


Figure 1.4: Average endpoints from the ‘healthy reef’ scenario in each of the five MAR subregions for benthic and consumer groups from five model runs of 100 years (error bars indicate 95% confidence intervals). Means were taken across subregions for: coral (brooding and spawning corals combined) and macroalgal covers (A); brooding and spawning coral covers (B); and herbivorous and piscivorous fish biomass (sum of small-to-intermediate and large piscivorous fish biomasses) (C). Differences in community composition between subregions are emergent from the model.

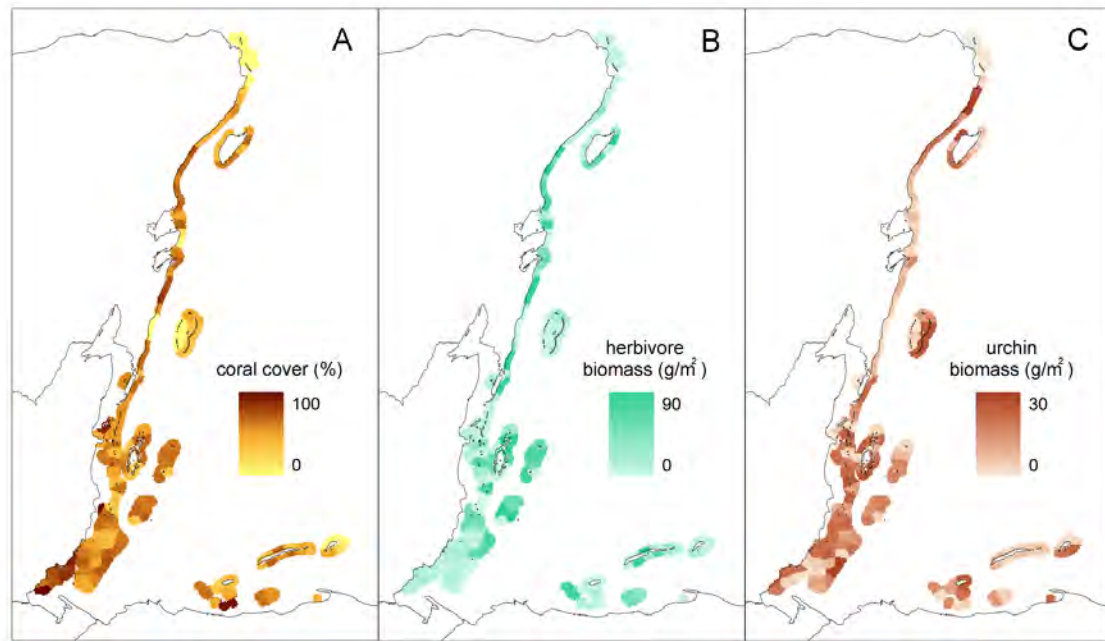


Figure 1.5: Spatial variation in modelled coral cover (A), herbivorous fish biomass (B) and sea urchin biomass (C) across the MAR for the ‘healthy reef’ scenario. For visualization purposes, values displayed are averages across cells within polygons at the final time step of a 100 year model run. Spatial variability within the region is pronounced and emerges as a result of variability in larval supply, and how this affects ‘downstream’ dynamics directly and indirectly.

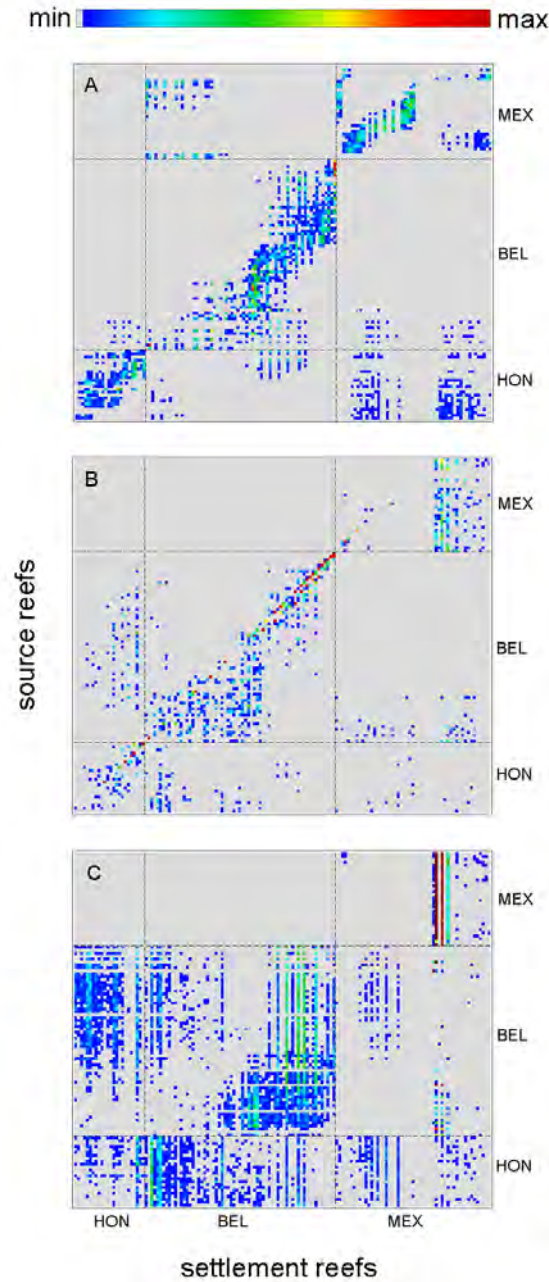


Figure 1.6: Matrices of transition probabilities between source reefs and settlement reefs for coral (A), fish (B) and sea urchin larvae (C). The matrix for coral larvae applies to spawning corals only; brooded coral larvae settle locally. Values are standardised relative to the maximum recruitment probability for each group. Dashed lines indicate spatial delineations for source and settlement reefs in Mexico (MEX), Belize (BEL) and Honduras (HON). Self-recruitment (represented on the upward diagonal axis of each plot) is strongest for fish and weakest for sea urchins. Predicted coral and fish larval supply is depauperate for some Mexican reefs.

Historical trajectories

Model trajectories from 1980 – present for the five MAR subregions showed reasonable correspondence with available data points for benthic and consumer functional groups (Figures 1.7 and 1.8). CORSET captured the widespread decline in coral cover and increase in algal cover in the MAR over the past 30 years which has been described qualitatively (e.g. Arrivillaga and Garcia, 2004) but is not well documented in quantitative terms. The impacts of hurricane and bleaching events are clearly evident in model trajectories for coral and algal cover (Figure 1.7) and it appears that the modelled effects of chronic stressors (fishing, nutrification and sedimentation) may have hampered recovery of coral cover following disturbance events. Data points for 2004 – 2005 (García-Salgado et al., 2006) are from sites within marine protected areas, so may reflect healthier reef states than average.

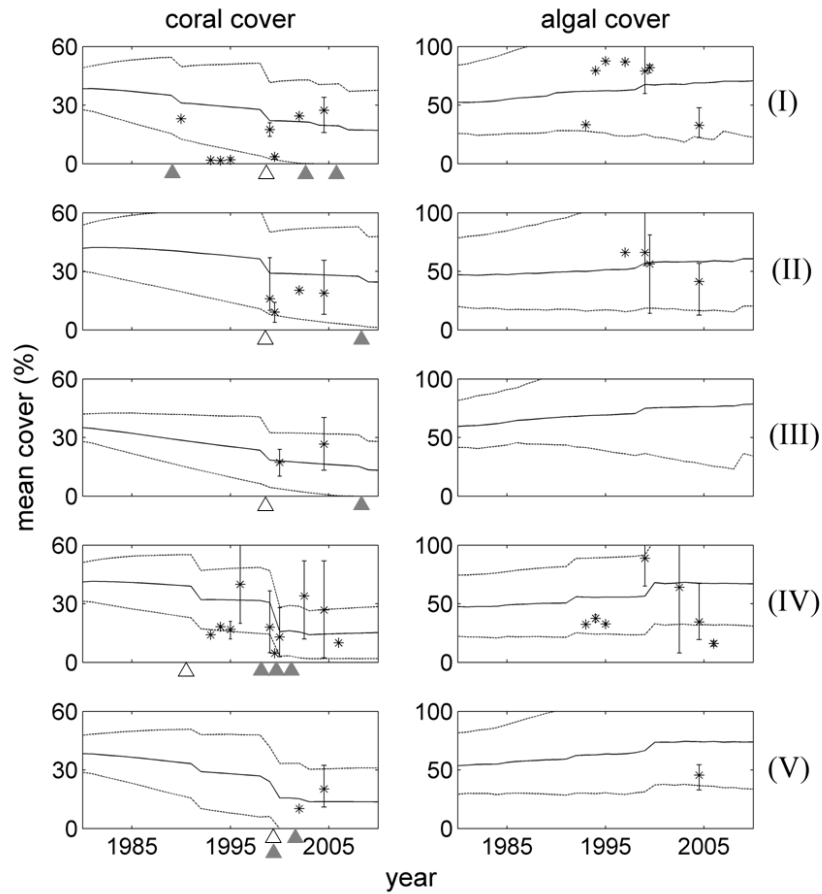


Figure 1.7: Comparison of model trajectories for coral and algal cover in the five MAR subregions from 1980 – present with empirical observations (see Table C1, Appendix C for a summary of empirical data sources). Solid lines indicate mean trajectories from five model runs, and dashed lines indicate 95% confidence intervals for cover and algal cover across all reef cells within each subregion. Vertical bars and stars indicate minimum-maximum ranges and average values from empirical observations, respectively. Algal cover refers to macroalgal and macro turf covers combined. Open triangles represent disease and bleaching events; closed triangles represent hurricanes. Empirical estimates of algal cover in subregion III were not available.

The biomass of large piscivores declined over the simulated time series, however data are not available to verify modelled biomass for this functional group separately. Our estimates of historical fishing pressure in Belize may have been too conservative as CORSET over-predicted herbivorous and piscivorous fish biomass in this subregion (Figure 1.8). Modelled historical piscivorous fish biomass was highly variable between reef cells in Belize, as reflected in large confidence intervals for piscivore biomass in this subregion. Model outputs indicated slightly better recovery of sea urchins in subregions I, III and IV than in subregions II and V following the major urchin disease mortality event in the early 1980s.

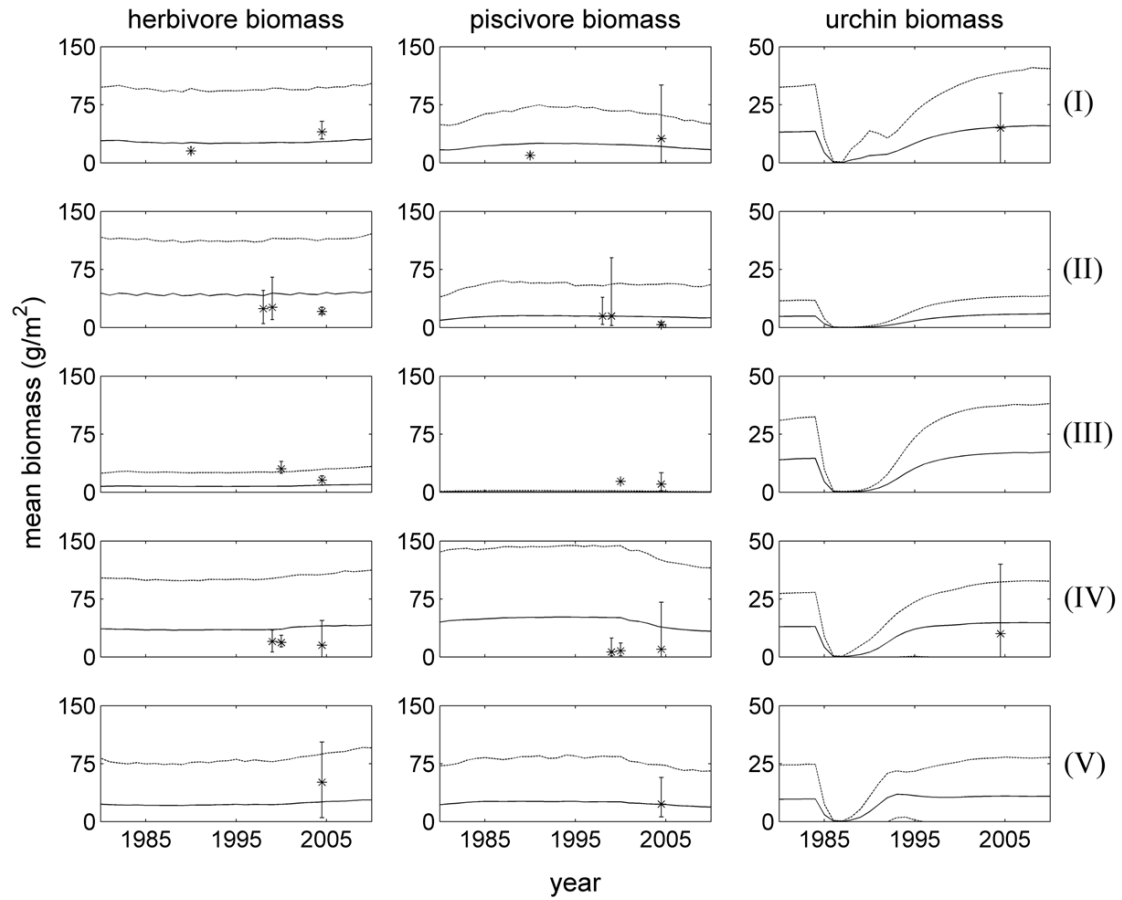


Figure 1.8: Comparison of model trajectories for herbivorous fish, piscivorous fish and sea urchin biomass in the five MAR subregions from 1980 – present with empirical observations (see Table C1, Appendix C for a summary of empirical data sources). Solid lines indicate mean trajectories from five model runs, and dashed lines indicate 95% confidence intervals for fish and sea urchin biomass across all reef cells within each subregion. Vertical bars and stars indicate minimum-maximum ranges and average values from empirical observations, respectively. Piscivorous fish biomass refers to the sum of small-to-intermediate and large piscivorous fish biomasses. Empirical estimates of sea urchin biomass in subregions II, III and V were not available.

1.4 Discussion

Model validation for the Meso-American Reef system: implications for coral reef management in the region

Coral reefs are complex multi-scale systems, with inherent properties of emergence, self-organization, and unstable equilibria that can be difficult to capture using models, but which nevertheless have significant implications for the management and conservation of reef ecosystems. In our regional-scale model (CORSET) we represent a complex reef system using a minimal set of biophysical processes and ecological interactions. We asked two questions of the model using an instantiation for the Meso-American Reef (MAR) system: could it simulate the expected quasi-equilibrium state of a healthy reef system in the absence of human impacts or disturbance? and how would the model respond to a scenario representing our best interpretation of disturbance events and anthropogenic impacts that have affected reefs in the MAR over the past 30 years? Despite its relatively simple structure and the limitations of comparing model output with sparse empirical data (resulting in the large confidence intervals for vertical bars in Figures 1.7 and 1.8), CORSET realistically captures broad dynamics for the MAR since 1980. Moreover, our examination of the model's behaviour under the 'healthy reef' scenario provides insights into inherent differences between subregions of the MAR that may influence real-world dynamics for this reef system.

The spatial variability we observed from the model at subregional and regional scales (Figures 1.4 and 1.5) is emergent; it arises from the complex nature of larval connectivity and cascading downstream effects of low or high recruitment. The dispersal and recruitment of marine larvae is fundamental to understanding, modelling and managing marine ecosystems (Gaines and Lafferty, 1995; Sale et al., 2005; Grober-Dunsmore and Keller, 2008), yet the study of these processes is a developing science. Here, by explicitly including larval connectivity information – from sophisticated particle transport simulations that include key elements of larval behaviour influencing transport – in our regional-scale model, we are able to directly evaluate some of the potential consequences of larval connectivity patterns across a range of spatial scales.

Our results indicate that reefs at the northern extreme of the MAR model domain receive fewer fish and coral larvae relative to more southerly reefs (Figure 1.6). These differences, if real, might confer vulnerability to repeated disturbance events. In our historical scenario, hurricane and bleaching events that affected reefs in the northern Mexican Caribbean between 1980 – present were intermittent compared with consecutive disturbance events in Belize and Honduras (Table 1.4 and Figure 1.7). However, the frequency of coral bleaching events and the frequency of intense Atlantic hurricanes are likely to increase in coming decades (Donner, 2009; Bender et al., 2010). Results from the historical scenario we examined also suggest that the presence of multiple chronic stressors may have hampered recovery of coral populations from disturbance events during the past 30 years (as has been demonstrated from coral growth records in the MAR region; Carilli et al., 2009a). CORSET can be used to decouple confounding effects of disturbance, coastal development and fishing on reef systems, and to assist the design of management strategies that minimise synergistic impacts.

The coral reef community composition predicted by CORSET for the offshore atoll Banco Chinchorro was distinct from other subregions in two respects; the dominance of brooding corals over

spawning corals and a relatively low fish biomass (both herbivorous and piscivorous fish). Results from our larval transport simulations for the MAR indicate that the supply of larvae from spawning coral species to Chinchorro is low compared with other subregions, and that the primary source reefs for supply of coral larvae to Chinchorro are in northern Belize and Honduras. Damage to reef systems in these ‘source’ locations – particularly in Honduras where further changes in land use practices could lead to severe sedimentation of adjacent reefs (Burke and Sugg, 2006) – may have significant consequences for the resilience of reefs on Banco Chinchorro. Hence, although the direct impact of sediments from Honduran river inputs is likely to be low on Chinchorro (Paris and Chérubin, 2008), indirect impacts ostensibly have the potential to be quite large given larval connectivities. This is an example of how CORSET can be used to examine the potential ecological consequences of scenarios relating to land use change in the MAR region (which are explored in detail in Chapter 3).

Overfishing has generally been cited as the cause of low piscivorous fish biomass on Chinchorro (Loreto et al., 2003). However our results suggest that exogenous larval supply and standing stocks of herbivorous and piscivorous fish may be naturally low for this atoll. CORSET does not consider the contributions of fish spawning aggregations or nursery habitats to recruitment dynamics. Spawning aggregations of the Nassau grouper *Epinephelus striatus* occur throughout the MAR region, including Chinchorro. These aggregations play a key role in population dynamics for *E. striatus* and there is significant evidence that spawning routes and aggregation sites are highly vulnerable to overfishing (Aguilar-Perera and Aguilar-Dávila, 1996; Heyman and Requena, 2003). Availability of nursery habitats, particularly mangrove forests, has been shown to increase the biomass of commercially important fish species in the Caribbean (Mumby et al., 2004). We advocate consideration of features such as spawning aggregations and nursery habitats, in tandem with our approach, in designing management strategies for reef systems.

Limitations

Communicating limitations and identifying sources of uncertainty are important considerations in designing and applying complex systems models, particularly where such models are intended for use in environmental decision making (Ascough II et al., 2008). Key limitations and sources of uncertainty in our approach are discussed here under three categories: (i) the limitations of using data from larval dispersal simulations, (ii) parameter uncertainty, and (iii) simplifying assumptions. Despite being highly informed by physical and biological data, connectivity patterns indicated by larval dispersal simulations should be interpreted with some caution unless validated by data from genetic or tagging approaches. Transport simulations for passive particles in the MAR derived from ROMS have been validated through comparison with ocean colour satellite data (Chérubin et al., 2008), but it is important to also include features of larval particles in estimating connectivity because, typically, estimates of transport of passive particles exaggerate larval dispersal distances (Cowen et al., 2000, 2006). However, connectivity strengths for active larval particles have been shown to be highly sensitive to assumptions regarding biological parameters, particularly larval survival and vertical migration (Paris et al., 2007). Furthermore, the transport simulations used here to inform CORSET were based on a single year’s worth of hydrodynamic simulations. Given that larval connectivity in nearshore systems has been shown to have a stochastic component in nature (Mitarai et al., 2008; Siegel et al., 2008), we would have greater confidence in interpreting

connectivity patterns and model output from CORSET given information from dispersal simulations over multiple years.

Sensitivity analysis provides a means to assess the implications of parameter uncertainty, and a detailed sensitivity analysis for CORSET is provided in Chapter 2. Results from this chapter indicate that modelled reef state is most sensitive to coral growth, coral death and piscivorous fish death rates, and to coral larval production. While there is some uncertainty in the estimation of all parameters in CORSET, estimates of larval production are particularly uncertain as published data for these values are sparse and variable and it is likely that larval production differs between biogeographic regions (e.g. because of differences in species compositions). Given the likelihood that larval production is region-specific, the sparseness of published estimates, and the fact that the model is sensitive to larval production parameters (at least for corals), we tuned the model by varying larval production within acceptable ranges derived from the literature (see Appendix B). Because information is not available on the nature of spatial variability in parameters for the MAR, we assumed random spatial variability in local model parameters. However all forcing parameters and connectivity information was entered in a spatially-explicit manner. CORSET is amenable to input of systematic inter-reef differences in parameters values where such information is available.

As in any modelling study we have made a range of simplifying assumptions in CORSET, the key ones being: (a) the selection of functional groups to model, (b) use of uniform distributions for parameters, (c) lack of seasonality in growth, reproduction and disturbance, and (d) assumptions regarding reef habitat characteristics in the MAR and the spatial variability of major forcings. Selection of functional groups was based on the minimum suite of groups we believed was necessary to capture essential coral reef structure and ecological processes on coral reef systems worldwide, acknowledging that species compositions can be very dissimilar across regions. We selected nine functional groups for which we were able to define a set of interactions that can be parameterised for reefs in different biogeographic regions, and which together provide a useful representation of reef state. The local model that defines interactions among these nine functional groups (see Appendix A) is arguably the most complex yet developed for coral reefs, but is nonetheless a gross simplification of dynamics among the myriad species that inhabit coral reefs. The addition of invertivorous fish as a tenth functional group may be appropriate for regions where this group is economically important, given that the model is intended as a decision support tool. Additionally, some management questions may extend to other habitats that are ecologically or functionally linked to coral reefs in some way, e.g. seagrass and mangrove habitats, but which are not currently captured in CORSET. Nonetheless, the architecture of CORSET is structured such that additional habitats and functional groups can be incorporated in a modular fashion.

We used uniform distributions for parameters in the absence of other information regarding the shape of distributions for ecological parameters in CORSET. This may exaggerate or dampen dynamics unrealistically if our parameter ranges (estimated largely from empirical observation) are larger than the typical range for ecological processes on coral reefs. Seasonality was not represented in CORSET because, with a focus on management at sub-regional scales, the model is intended for simulations over decadal time scales and parameter values represent yearly averages rather than seasonal processes. A disadvantage of this approach is that in real reef systems ecological thresholds need only be crossed for short periods for them to have long term consequences; CORSET is limited in its ability to resolve this kind of dynamic change.

Finally, we have made simplifying assumptions about the characteristics of coral reef habitats and the impacts of forcings such as fishing pressure and nutrification/sedimentation across the MAR region. Our approach assumes that all reef cells in the model domain can support coral cover. This is reasonable given the high quality of source data for our MAR base map (i.e. 30 m Landsat imagery; IMaRS, 2004) and the fact that only geomorphological classifications with a high probability of being living coral (forereef, reef flat, barrier reef pinnacle and shallow terrace) were included in the base map (as in Burke et al., 2004). However, our approach is not able to resolve the diversity of reef habitats within the MAR (which according to Kramer and Kramer 2002 is substantial) beyond emergent differences in community structure as determined by differing abundances of modeled functional groups. The spatial representation of major forcings in our historical trajectories – in particular fishing pressure and nutrification/sedimentation impacts – is also simplistic. While the impacts of these forcings do vary in space and time in the model, limited information was available regarding systematic differences in the impacts of these forcings over the MAR region during the past 30 years. As a result, we have been reasonably cautious in our interpretation of spatial patterns in reef state that emerge from the model. While our use of simplifying assumptions is appropriate for the general purposes of demonstrating CORSET, testing the model's behavior and assessing broad-scale patterns in model results, the model architecture allows more realistic patterns of reef distribution and anthropogenic impacts to be built into future instantiations.

Despite these caveats, CORSET was nonetheless able to realistically capture broad dynamics for the MAR and to reproduce changes in variables that are of interest to coral reef managers and other stakeholders. Some of the issues we have raised in relation to limited data availability can possibly be overcome using alternative approaches such as Bayesian Belief Networks (BBNs, e.g. Wooldridge and Done, 2004; Wooldridge et al., 2005; Renken and Mumby, 2009), although BBN approaches may be less transparent for non-scientist end users and existing BBN applications for coral reef systems are not spatially explicit. Importantly, the most robust management and associated decision support will attempt to utilize a toolbox of several model types. Even with its limitations, the behavior of CORSET indicates that it would be a useful component of that toolbox.

Potential management applications

CORSET provides an adaptable framework for scenario projection to support decision making in relation to the conservation and management of coral reef systems. Potential applications include identifying the synergistic effects of multiple disturbance events that occur simultaneously or sequentially (for example, the degree to which nutrification and sedimentation hamper recovery of coral cover following hurricane disturbances) and the effects of chronic anthropogenic disturbances and/or stressors. CORSET can be used to estimate the likelihood of potential reef futures under different management strategies, and hence evaluate risks associated with different courses of action. For example, it could be used to assess whether it is more risk averse to prioritise regulation of fishing activity over coastal development. Our model could also facilitate comparisons of the effectiveness of particular management approaches between regions. Important applied questions such as these are sensibly focused at spatial scales well beyond the scope of conventional experimental and observational approaches.

While the emphasis of our study, and of previous efforts to model coral reefs (e.g. McClanahan, 1995; McCook et al., 2001; Mumby, 2006b; Mumby et al., 2006; Holmes and Johnstone, 2010), has been on biophysical scenarios and responses, scenario projection is arguably most informative for management and policy making when it addresses linked biophysical-socioeconomic dynamics (e.g. Gray et al., 2006; Shafer, 2007) and captures both socioeconomic and biophysical indicators of reef state (Hatzios et al., 2006; McField and Richards-Kramer, 2007). Agent-based modelling approaches have been applied successfully to model populations of marine resource users, and to evaluate strategies for managing multiple extractive activities (Gray et al., 2006). The forcings we applied in our study to recreate an historical scenario for reefs in the MAR (physical damage, harvesting, nutrification and sedimentation) can be used as ‘pipes’ for information transfer between CORSET and an agent-based socioeconomic model (as is demonstrated in Chapter 5). As a stand-alone model or in tandem with a dynamic socioeconomic model, CORSET has important applications as a tool for decision support in the management of coral reef systems. In the near future we can hope to see scenario projection integrated with existing approaches for vulnerability assessment, marine reserve design and reef state visualization to inform the difficult task of effective management of complex coral reef systems.

Chapter 2

Characterising sensitivity and uncertainty in a model of a complex coral reef system

Abstract

Sensitivity and uncertainty are intrinsic properties of ecological models, and their characterisation is an important step in the modelling process. We use a spatially explicit multi-scale model of a coral reef system to explore four aspects of model sensitivity and uncertainty: (i) sensitivity to initial conditions; (ii) sensitivity to parameter values; (iii) sensitivity to spatio-temporal resolution; and (iv) the effects of uncertainty about spatio-temporal variability of ecological processes on the shape of distributions of model predictions. We use reef community composition, visualised in multivariate space, as a response variable. This approach provides an easily interpretable representation of changes in reef community composition under different parameter conditions and spatio-temporal resolutions. It is also a useful means for visualising distributions of model outcomes under differing assumptions about the nature of variability in ecological processes in the real world. Our results indicate that reef state and recovery trajectories are particularly sensitive to parameters determining coral growth and mortality rates. Variability in model outcomes depends on assumptions about the way parameters vary in space and time, and is greater at local scales than at subregional and regional scales. Our findings suggest that model predictions are likely to be more robust for subregions and regions than for particular reef localities.

2.1 Introduction

In ecological modelling, sensitivity refers to the relative importance of input factors in determining model outputs, while uncertainty refers to incomplete knowledge about the components and processes of the system being modelled. In practice these concepts can overlap, since the parameters to which a model is sensitive can also be uncertain. Identifying sensitivities and sources of uncertainty is an important step in model building and is requisite in designing and assessing the applicability of complex systems models (Monte et al., 1996; Cariboni et al., 2007; Ascough II et al., 2008; McElhany et al., 2010). Moreover, it assists in identifying knowledge gaps for research prioritisation. While sensitivity analyses for ecological models have conventionally focused on the importance of model parameters in influencing model outcomes (Jørgensen, 1994), a growing body of literature on uncertainty analysis underscores the raft of other factors to consider in characterising model behaviour and assessing the reliability of model predictions (Li and Wu, 2006; Lek, 2007; Clancy et al., 2010) including spatial resolution and model structure.

The choice of spatial resolution in environmental models can significantly affect model predictions (Heuvelink, 1998), and similarities between predictions across scales can break down when forcings are introduced (Murray, 2001; Fulton et al., 2004). Temporal resolution, or the choice of a model time step, can also influence model outcomes. Meaningful event scheduling, which is particularly important for spatially explicit models (Ruxton and Saravia, 1998) relies in part on the choice of an ecologically relevant model time step. The use of alternative model structures, usually reflecting different assumptions, is an uncertainty seldom assessed, but can account for more than half of the overall variance in simulation outcomes (Valle et al., 2009). Alternative assumptions about the way that parameters vary in space and time, which reflect uncertainties about variability in ecological processes in the real world, can have important consequences for the shape of distributions of model predictions.

In the current study, our aim was to characterise variability in model predictions under steady-state and non-steady-state conditions, and to identify inputs and assumptions that have a strong influence on the portion of phase space occupied by model dynamics. We used a spatially explicit multi-scale model of a coral reef system – CORSET (Coral Reef Scenario Evaluation Tool; Melbourne-Thomas et al., 2010, in press) – to address these questions. Coral reefs are complex systems, with a range of biophysical processes acting at different scales in space and time. CORSET distils this complexity by using a functional group approach and coupling dynamics from local (10^2 m) to regional (10^6 m) scales via larval connectivity. Local-scale ecological dynamics are modelled in each reef cell of a gridded base-map using a set of difference equations, with reef cells connected by regional-scale larval dispersal and recruitment. The model framework is generic and can be applied to reef systems in different biogeographic regions. It is designed to be used in decision support for coral reef management. CORSET has been instantiated and validated for two reef systems; the Meso-American Reef system in the western Atlantic (Chapter 1) and the Philippines region of the South China Sea (Chapter 4). Here, we use the model for Meso-America as a test case (see Figure 2.1B for a map of the modelled area).

We examine four aspects of model sensitivity and uncertainty:

- (i) sensitivity to initial values of state variables,
- (ii) sensitivity to parameter extremes,
- (iii) sensitivity to spatial resolution and the length of the model time step, and
- (iv) the effects of uncertainty about spatio-temporal variability of ecological processes on the shape of distributions of model predictions.

Klepper (1997) describes the use of multivariate techniques for grouping ‘modes’ of model behaviour under different parameter configurations. Here we use principal components analysis (PCA; Chatfield and Collins, 1980) to visualise reef state under different modelling assumptions. Reef state is defined by the relative values of state variables in the model. State variables include: (a) the proportional covers of five benthic functional groups – brooding and spawning corals (jointly referred to as ‘corals’), macroturf, macroalgae and epilithic algal communities (EAC) – and (b) biomasses of four consumer functional groups – herbivorous fish, small-to-intermediate piscivorous fish, large piscivorous fish and grazing sea urchins. Definitions and examples of these functional groups are provided in Table 1.1 (Chapter 1). In our analyses of (i) sensitivity to initial values, (ii) sensitivity to parameter extremes, and (iii) spatio-temporal sensitivities (all of which are addressed in Section 2.2), reported values for reef state refer to regional-scale averages, i.e. averages across all reef cells in the model domain. Section 2.3, which examines the effects of different model formulations – specifically, different schemes for varying parameter values in space and time – on the shape of distributions of model predictions, presents model output at regional and subregional scales, and at the local scale of individual reef cells.

2.2 Sensitivity

Initial conditions

Initial conditions were varied across a range of covers and biomasses for benthic and consumer groups respectively. We examined trajectories of 150 years to determine sensitivity to initial conditions and time to reach a steady-state. Initial values tested for coral cover, macroalgal cover and macroturf cover were 1%, 30%, 60% and 90%, and for herbivorous fish, piscivorous fish (small and large piscivores combined) and sea urchins the initial biomass values used were 5g/m², 20g/m², 40g/m² and 60g/m² (which is the maximum reported herbivorous fish biomass for the region; Arias-González, 1998). CORSET reached a steady state under all combinations of initial conditions (Figure 2.2). The time taken for the model to reach a steady state was faster for consumer state variables (Figure 2.2B) than for benthic state variables (Figure 2.2A). The steady-state level of coral cover was $\sim 5\%$ lower, and macroturf cover $\sim 3\%$ higher under scenarios of low initial coral cover (i.e. initial coral cover = 1%), compared with scenarios where initial coral cover was $\geq 30\%$.

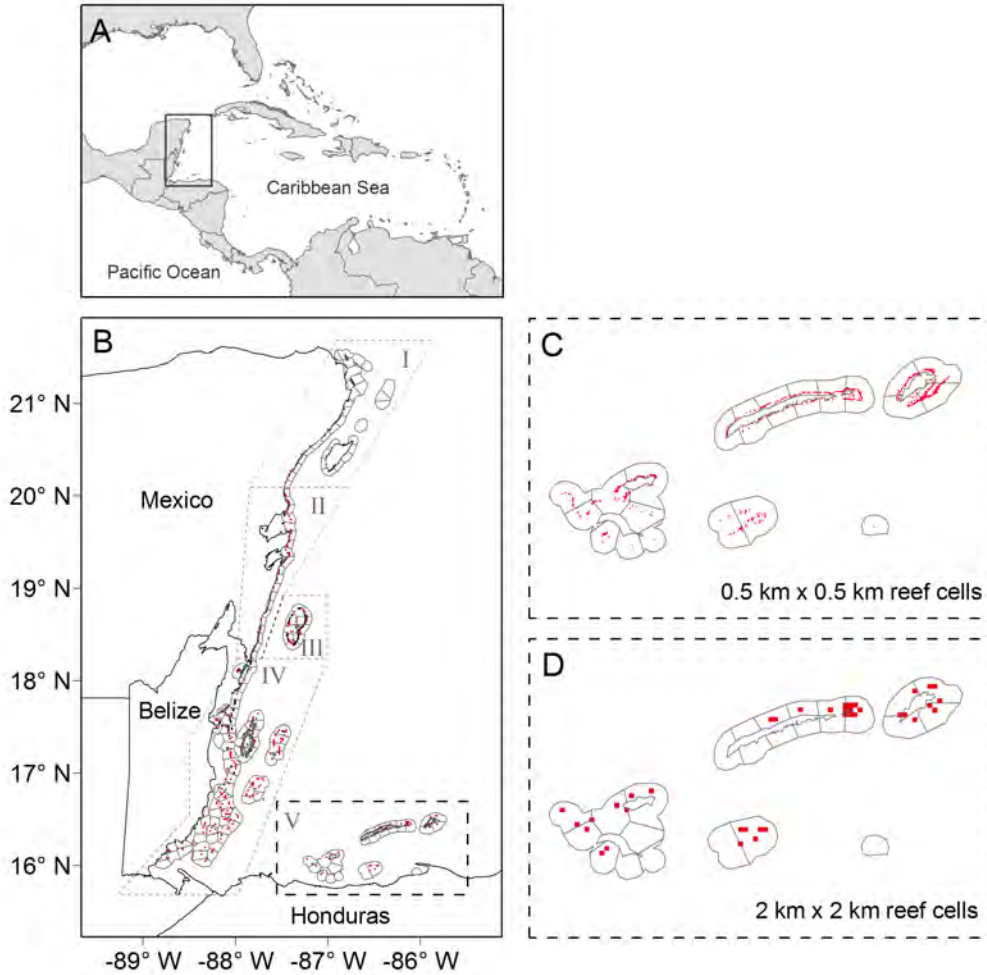


Figure 2.1: Spatial extent of the region modelled for the Meso-American Reef system instantiation of CORSET. Coral reef cells are indicated in red (the location of these cells is from IMArs, 2004) and are enclosed within connectivity polygons which are in the order of $5 \text{ km} \times 10 \text{ km}$. Five subregions are delineated by grey dashed lines in (B). (C) and (D) illustrate cases where connectivity polygons in Honduras (subregion V) contain reef cells at a fine spatial resolution ($0.5 \text{ km} \times 0.5 \text{ km}$ reef cells in C), but not at a coarse resolution ($2 \text{ km} \times 2 \text{ km}$ reef cells in D). The total area of reef is approximately equal at both resolutions.

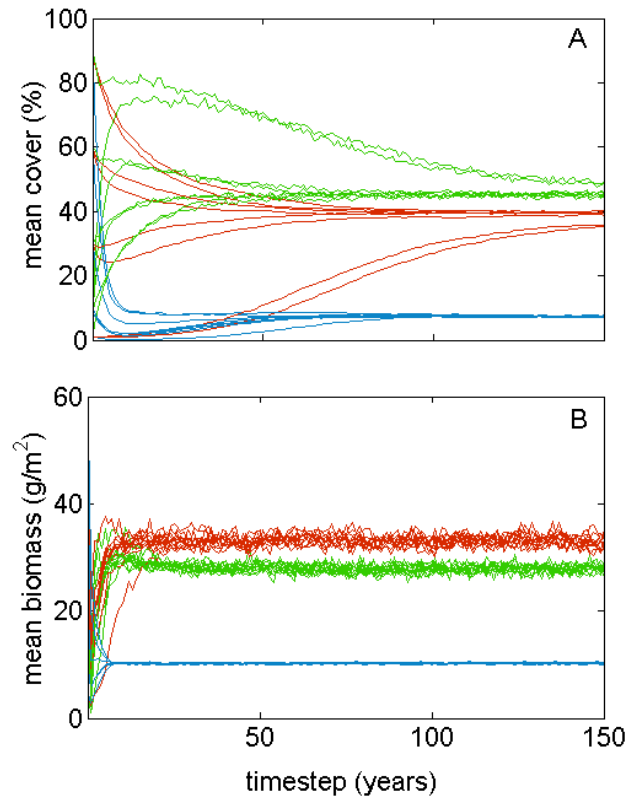


Figure 2.2: Model trajectories under varying initial conditions for (A) benthic state variables and (B) consumer state variables. In (A), macroturf cover is represented in green, coral cover in red and macroalgal cover in blue. In (B), piscivorous fish biomass (the sum of small-to-intermediate and large piscivorous fish biomasses) is represented in red, herbivorous fish biomass in green and sea urchin biomass in blue. There is greater variability in end points for benthic state variables than for consumer variables.

Parameter sensitivity

Two complementary approaches were used to examine parameter sensitivity in CORSET. The first of these – a ‘parameter limits’ analysis – gives an overview of model behaviour and identifies parameters that have high leverage, i.e. those parameters to which modelled reef state is particularly sensitive. Each biological parameter in the model was adjusted to both its lowest and highest plausible level (see Table A1, Appendix A) following Mumby (2006b). For parameter estimates that are single values (rather than ranges) we took $\pm 10\%$ of these values as the range for parameter testing. Three model runs of 150 years were conducted for both the fixed minimum and maximum values of each parameter, with all other parameters selected randomly from their predefined ranges at each yearly time step and for each reef cell. We examined community state (visualised in principal components space using PRIMER v6; Clarke and Gorley, 2006) as the response variable. Sensitivity analysis is typically classified as local (parameter values are varied one at a time) or global (groups of parameters are altered simultaneously; Cariboni et al., 2007). Our method can be considered as intermediate between a local and global sensitivity analysis because, although parameters are

examined singly, all other model parameters are allowed to vary randomly. The justification for taking this approach is twofold; first, it allows the full range of possible model behaviours to be examined, and second, it mimics the default behaviour of the model. The disadvantage is that additive and interactive effects of parameters on system dynamics cannot be quantified.

In our second approach to examining parameter sensitivity we introduced a coral bleaching disturbance (60% coral mortality) and compared the recovery capacity of the modelled reef system under different parameter scenarios (following Preece and Johnson, 1993). We looked at modelled reef recovery under minimum and maximum values of ten high leverage parameters identified from the ‘parameter limits’ analysis. If parameters have a strong influence on community composition under steady-state conditions *and* influence recovery trajectories then there is good evidence of high sensitivity for these parameters. If these sensitivities translate to the real world, then insights into recovery trajectories under certain parameter conditions may have implications for improving reef resilience to disturbance.

Results for parameter sensitivity under the ‘parameter limits’ analysis are presented separately for benthic, consumer, larval and forcing parameters (Figures 2.3, 2.4A, 2.4B and 2.5 respectively). Parameters were classified in terms of the state variable for which they represent an ecological process, for example ‘coral’ parameters are coral growth (r_C), coral mortality (d_C), growth of coral over macro turf (α_C) and recruitment of coral onto macro turf (ϵ_C ; see Table A1, Appendix A). Because the units for benthic state variables (%) and consumer state variables (g/m^2) differ, all principal components analyses were conducted using normalised reef state data.

From the principal components analysis of reef community composition under minimum and maximum values of benthic parameters, reef state is most sensitive to coral growth rate, coral mortality rate and the growth rate of coral over macro turf (Figure 2.3). We identify these parameters – which are associated with outlying points in principal components ordinations of modelled community composition – as having high ‘leverage’. Also evident from the principal components ordination is variation in reef state from high coral cover to low coral cover along PC1, and orthogonal variability along PC2 from high to low macroalgal cover. Parameters that drive high macroalgal cover relate to the competitiveness of macro turf (ζ_T and g_T ; see Table A1, Appendix A); macroalgal cover is high when macro turf is less competitive. These parameters do not have high leverage.

Principal components ordination of reef community composition under fixed minimum/maximum values of consumer parameters (Figure 2.4A) indicates orthogonal axes of: (i) benthic community composition (PC1), varying from high coral cover to high algal cover, and (ii) variation in fish community composition (PC2), from dominance by piscivorous fish to dominance by herbivorous fish. High leverage consumer parameters are the death rate (due to natural mortality) of herbivorous and piscivorous fish and grazing accessibility for herbivorous fish and sea urchins (Figure 2.4A). The ordination of reef community state under larval parameter limits is defined by orthogonal axes of coral-dominated versus macro turf/EAC-dominated benthos, and high grazer biomass versus high macroalgal cover (Figure 2.4B). Coral fecundity and the density-dependent mortality rate for fish and sea urchin recruits are identified as high leverage larval parameters in Figure 2.4B.

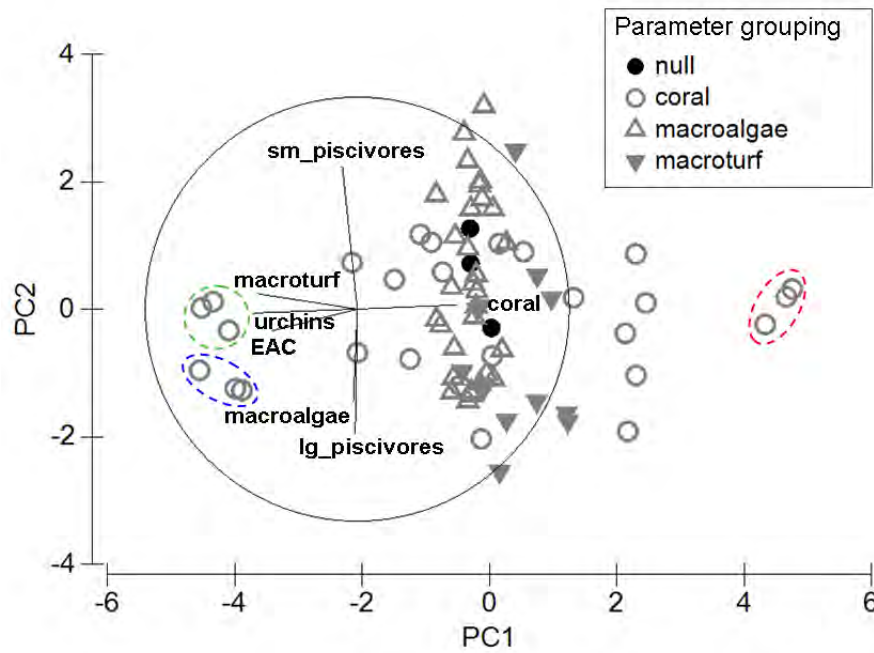


Figure 2.3: Principal components ordination of reef community state under extreme values of benthic parameters. Average reef state after 100 years is presented from three model runs for each benthic parameter fixed at its minimum or maximum value. Under the ‘null’ case all parameters are allowed to vary randomly within their predefined ranges (Table A1, Appendix A). Radiating lines indicate state variable vectors (eigenvectors). 67% of the total variance is captured by PC1 (48%) and PC2 (19%). Notable outliers are indicated by dashed circles; red = minimum coral mortality, green = minimum coral growth rate, and blue = minimum coral growth rate over macroturf. EAC is epilithic algal community and small-to-intermediate and large piscivorous fish are abbreviated as sm_piscivores and lg_piscivores, respectively.

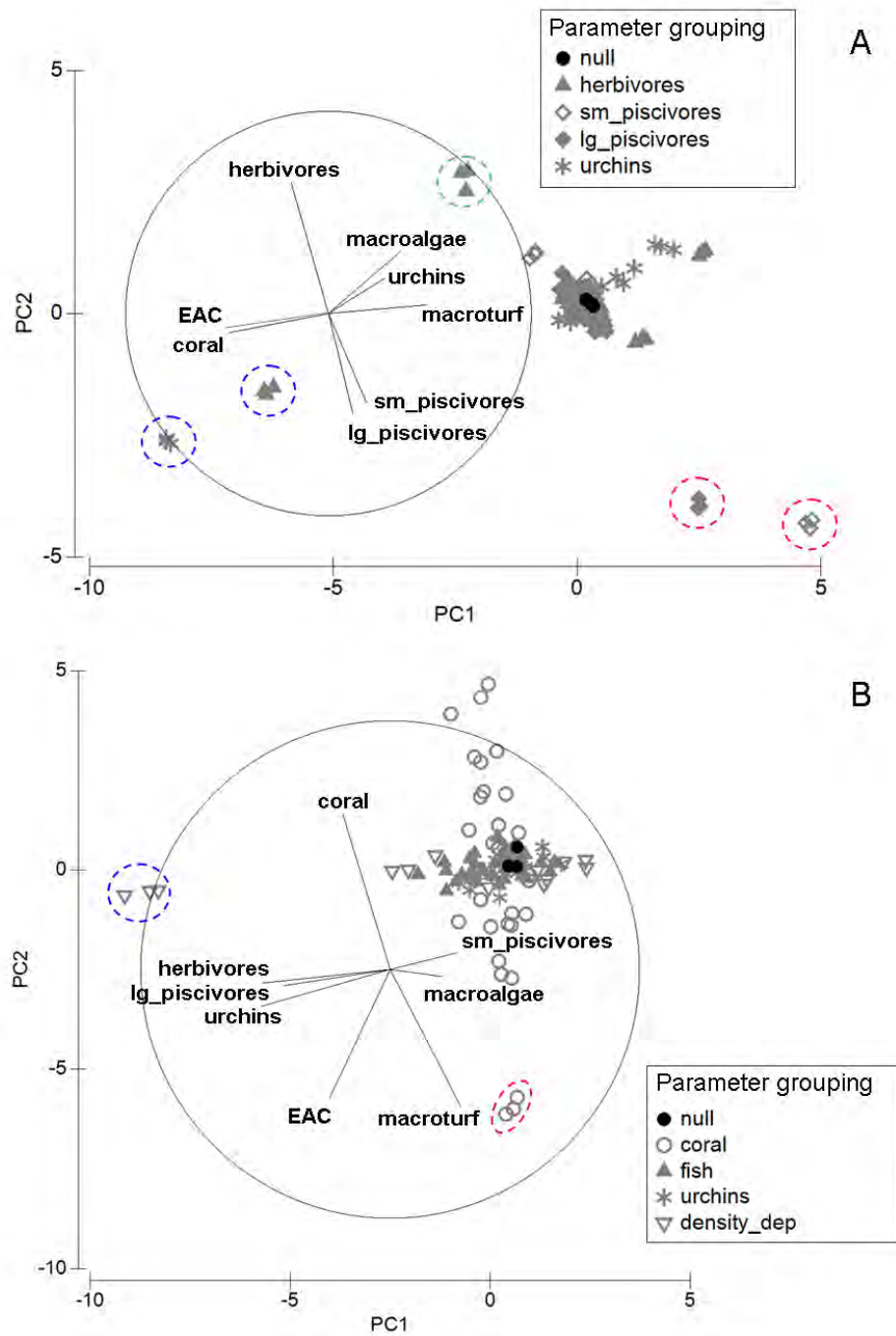


Figure 2.4: Principal components ordination of reef community state under extreme values of (A) consumer parameters and (B) larval parameters. Average reef state after 100 years is presented from three model runs for each parameter fixed at its minimum or maximum value. Under the ‘null’ case all parameters are allowed to vary randomly within their predefined ranges. In (A) 67% of the total variance is captured by PC1 (49%) and PC2 (18%) and in (B) 65% of the total variance is captured by PC1 (36%) and PC2 (29%). Notable outliers are indicated by dashed circles. In (A), red = minimum mortality for piscivorous fish, green = minimum mortality for herbivorous fish, and blue = maximum grazing accessibility. Fish mortality refers to natural mortality from all factors excluding fishing and predation. In (B), red = minimum coral fecundity, and blue = minimum density-dependent mortality for fish and urchin recruits.

In examining the sensitivity of reef state to forcings parameters (i.e. the ecological effects of nutrification, sedimentation and fishing, see Table 1.3, Chapter 1) the ‘null’ state represents an altered reef which is under pressure from chronic stressors (Figure 2.5). The greatest change to this altered reef community composition occurred at minimum and maximum values of the scaling factor for coral death rate under sedimentation. This is in agreement with results presented for benthic parameter sensitivity, where coral death rate (d_C) was identified as an important parameter in determining community state (Figure 2.3).

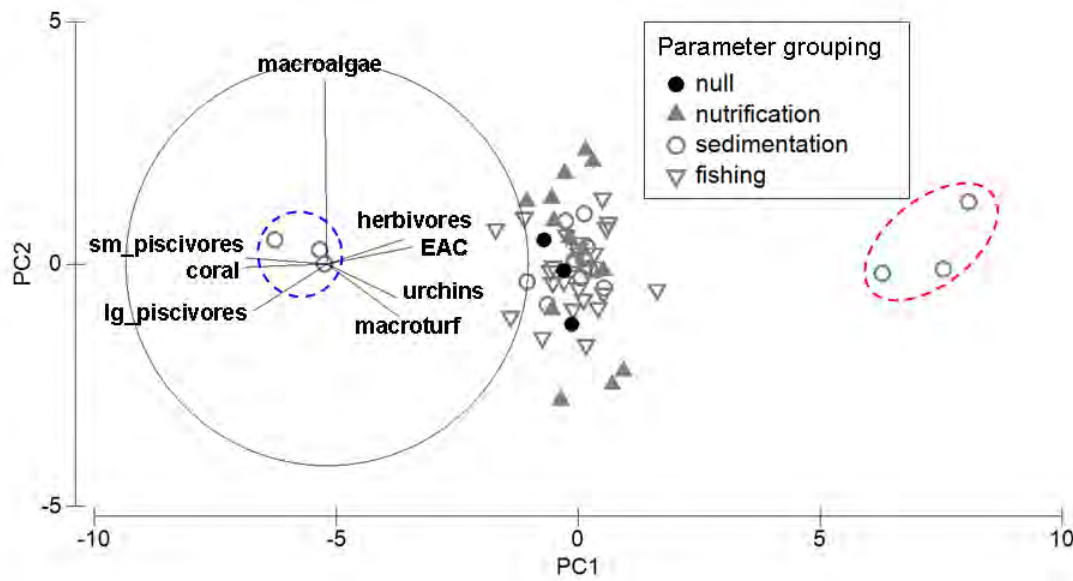


Figure 2.5: Principal components ordination of reef community state under extreme values of forcing parameters (i.e. the ecological effects of nutrification, sedimentation and fishing, see Table 1.3, Chapter 1). Average reef state after 100 years is presented from three model runs for each parameter fixed at its minimum or maximum value. Under the ‘null’ case all parameters are allowed to vary randomly within their predefined ranges. 75% of the total variance is captured by PC1 (62%) and PC2 (13%). Notable outliers are indicated by dashed circles; red = maximum increase in coral mortality under sedimentation, and blue = minimum increase in coral mortality under sedimentation.

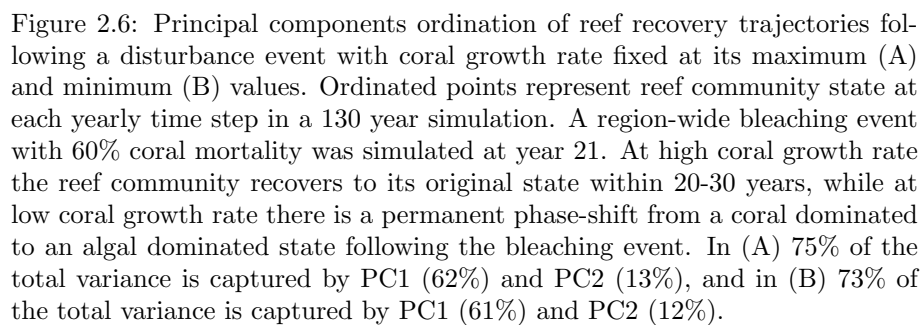
We examined reef recovery trajectories following a severe coral mortality event under the minimum and maximum values of high leverage parameters identified from Figures 2.3 and 2.4 (high leverage parameters are listed in Table 2.1). We did not examine sensitivity of recovery trajectories to high leverage forcing parameters (Figure 2.5) because (a) reef state under model forcings is already perturbed (i.e. we cannot apply a controlled perturbation), and (b) the forcing parameter identified as having the highest leverage was the scaling factor for coral mortality under sedimentation. Recovery trajectories under extreme values for coral mortality are already included in the perturbation analysis (see Table 2.1).

Reef state recovered to a coral-dominated condition over a period of 20-50 years under some parameter conditions (e.g. Figure 2.6A), while others trajectories were characterised by a phase-shift from a coral-dominated to an algal-dominated reef state (e.g. Figure 2.6B). These behaviours are summarised in Table 2.1. Interestingly, model runs under minimum values for the death rate of small-to-intermediate and large piscivorous fish took longer to reach an initial steady state. In examining recovery trajectories for these parameters the coral mortality event was scheduled to occur later (at year 61 rather than year 21), to allow the reef community to reach a steady state before being perturbed. Under minimum death rates for piscivorous fish, herbivorous fish biomass was depauperate and the system reached a new stable state with high algal cover following coral mortality associated with bleaching. Coral parameters (growth rate, mortality and fecundity) were important in determining the likelihood of phase-shifts. If this finding translates to the real world then it has implications for reef management, as coral life history parameters are modified by anthropogenic stressors such as nutrification and sedimentation (Table 1.3, Chapter 1); effective management of these stressors is likely to increase the resilience of reef systems to disturbances such as coral bleaching mortality.

Table 2.1: Summary of recovery responses for modelled reef communities following a coral bleaching event under minimum and maximum values for high leverage parameters. A tick (✓) indicates that the modelled community underwent a phase-shift following the bleaching event (e.g. Figure 2.6B), while a cross (✗) indicates that the modelled reef community recovered to its original state following the bleaching event (e.g. Figure 2.6A).

	Minimum	Maximum
Benthic parameters		
Coral growth rate (r_C)	✓	✗
Coral death rate (d_C)	✗	✓
Growth of coral over macro turf (α_C)	✓	✗
Consumer parameters		
Death rate of herbivorous fish (d_H)	✗	✗
Death rate of small-to-intermediate piscivorous fish (d_{P_s})	✓	✗
Death rate of large piscivorous fish (d_{P_l})	✓	✗
Accessibility of algae to herbivorous fish grazing*	✓	✗
Accessibility of algae to sea urchin grazing*	✗	✗
Larval parameters		
Coral fecundity	✓	✗
Density-dependent mortality rate for fish and urchins	✗	✗

*Accessibility of algae to herbivorous fish and sea urchin grazing is represented in the local model by the *inverse* accessibility terms i_H and i_U (see Appendix A), hence minimum accessibility to grazing actually occurs when i_H and i_U are maximal, and maximum accessibility occurs when these parameters are at their minimum values.



Spatial resolution

Validation of CORSET for the Meso-American Reef system (described in Chapter 1) was conducted using a high-resolution base-map, with coral reef grid cell dimensions equal to $0.5 \text{ km} \times 0.5 \text{ km}$. Here, we compare the behaviour of the model at base-map resolutions of $0.5 \text{ km} \times 0.5 \text{ km}$, $1 \text{ km} \times 1 \text{ km}$ and $2 \text{ km} \times 2 \text{ km}$. The mechanics of coupling spatially explicit larval connectivity information to local-scale dynamics in the Meso-American Reef system instantiation of CORSET leaves the potential for distortion in dynamic behaviour as the spatial resolution changes. Connectivity is defined as the probability of larval dispersal between reef polygons with average dimensions $5 \text{ km} \times 10 \text{ km}$, i.e. a spatial scale larger than the scale of coral reef cells in the model base-map (Figure 2.1C and D). Connectivity information is translated into recruitment dynamics in CORSET by:

- (i) Accumulating larval production (from spawning events) from all reef cells in each reef polygon;
- (ii) Modelling larval dispersal between polygons using information from Lagrangian Stochastic particle tracking models (Paris et al., 2007); and
- (iii) Dividing larvae that arrive at a particular sink polygon equally between all reef cells in that polygon.

In changing the resolution of reef cells, for example from $0.5 \text{ km} \times 0.5 \text{ km}$ to $1 \text{ km} \times 1 \text{ km}$, it is sensible to use a spatial re-sampling algorithm that preserves total reef area (such as ‘nearest neighbour’ assignment; ESRI, 2006), rather than allowing total reef area to be inflated at the coarser resolution (as is the case with the ‘majority’ re-sampling algorithm; ESRI, 2006). However, a consequence of preserving total reef area in spatial re-sampling is that the number of reef cells contained within each connectivity polygon changes (Figure 2.1). As the number of ‘occupied’ polygons decreases (at coarser resolutions) there are fewer larval sources, on average, for any particular reef cell. Hence there is a potential for model predictions to differ between spatial resolutions.

Principal components ordination of reef community composition at different spatial resolutions indicates differences in steady-state composition between resolutions and greater variability in modelled community state at coarser resolutions (Figure 2.7). However, these differences can be considered as ecologically non-significant (Figure 2.8). We found no qualitative differences in simulated recovery trajectories following a severe bleaching disturbance between the different spatial resolutions; this was true at both the regional and subregional level. Again, quantitative differences can be considered as ecologically non-significant.

Temporal resolution

Previous coral reef models have used updating time steps ranging from 20 days (McClanahan, 1995) to 6 months (Mumby, 2006b; Mumby et al., 2006). CORSET uses a discrete time step, as opposed to the local model described by Fung (2009) which uses differential equations and so is continuous. We distinguish between a yearly time step (for which model output is recorded) and the model updating interval (the ‘sub’ time step for updating the local ecological model), which can be specified by the user but which has a default value of one week. A small updating interval

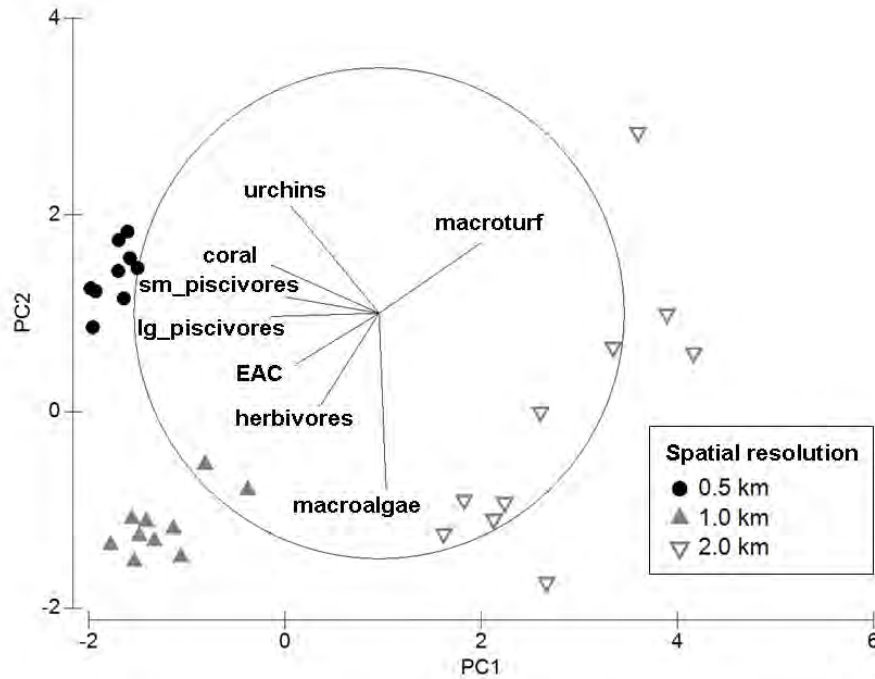


Figure 2.7: Principal components ordination of steady-state community composition from 10 Monte Carlo simulations at different spatial resolutions; 0.5 km \times 0.5 km, 1 km \times 1 km and 2 km \times 2 km grid cells. Community composition is more variable at coarse resolutions. 80% of the total variance is captured by PC1 (58%) and PC2 (22%).

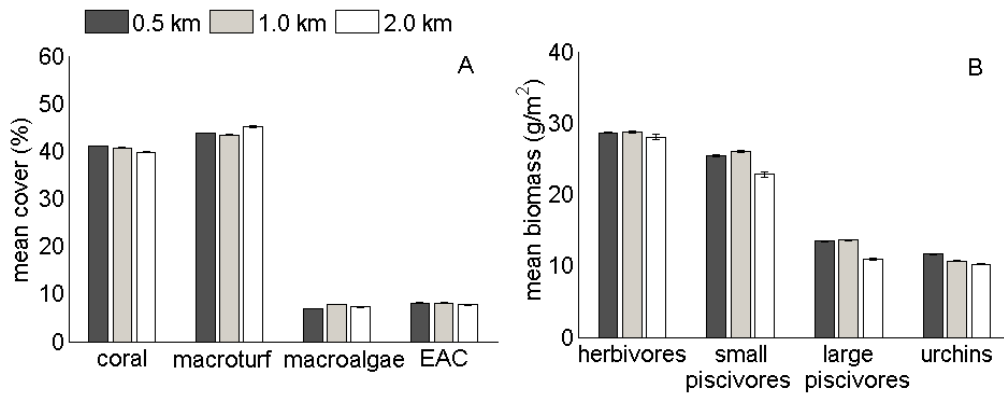


Figure 2.8: Average steady-state values for (A) benthic and (B) consumer state variables from 10 Monte Carlo simulations at different spatial resolutions; 0.5 km \times 0.5 km, 1 km \times 1 km and 2 km \times 2 km grid cells. Differences in community composition between spatial resolutions are ecologically non-significant.

better approximates the continuous version of the local model described by Fung (2009) and so requires fewer mathematical constraints to keep state variables within the biological domain, i.e. in the range 0 – 100% for benthic covers and ≥ 0 (but not tending to infinity) for consumer biomasses (T. Fung and R. Seymour, pers. comm.). However, small updating intervals are costly in terms of model run-time which poses a trade-off between efficiency and accuracy.

We compared model behaviour under daily, weekly, fortnightly, monthly and yearly updating intervals. Behaviour is characterised by (i) the proportion of runs for which dynamics go outside the biological domain (i.e. outside the range 0 – 100% for benthic covers and < 0 or tending to infinity for consumer biomasses) and (ii) differences in steady-state community composition under different updating intervals. Under yearly and monthly updating intervals model dynamics went outside the biological domain in 100% of runs, whereas for fortnightly, weekly and daily intervals all runs were within the biological domain. This behaviour suggests a tolerance threshold in terms of the length of the updating interval. There were no detectable differences in steady-state community composition under fortnightly, weekly and daily updating intervals.

The use of a discrete time step confers flexibility in terms of event scheduling. We examined differences in model behaviour for: (i) the case where coral, fish and sea urchin spawning and recruitment occurs evenly throughout the year (the default scheme in CORSET); and (ii) imposed seasonality in reproduction. Introducing seasonal spawning and recruitment required re-calibration to produce a steady-state reef community composition similar to yearly-averaged recruitment and spawning (Figure 2.9). Under seasonal reproduction it was necessary to force dynamics to be within the biological domain, i.e. to truncate fish and sea urchin biomasses at zero to prevent the model simulating negative biomasses. This is undesirable in terms of mathematical rigour.

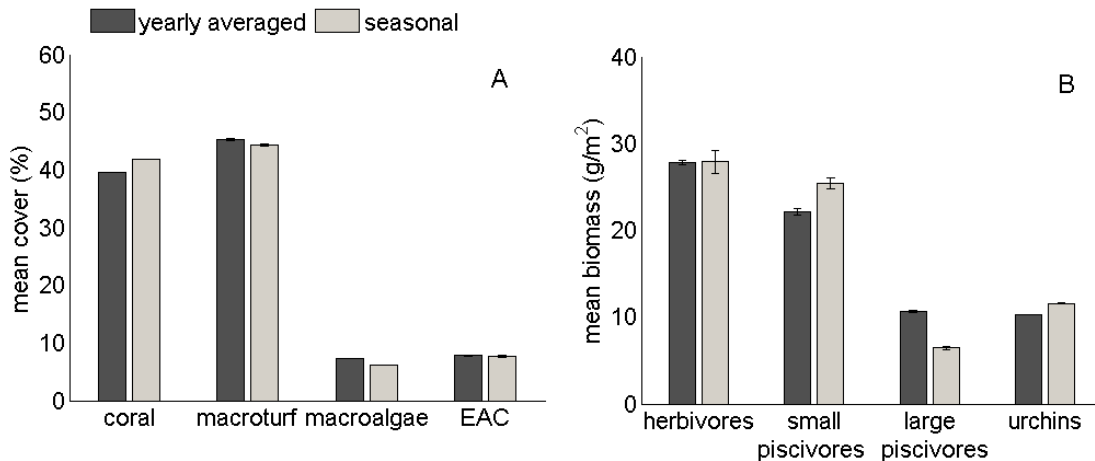


Figure 2.9: Average steady-state values for (A) benthic and (B) consumer state variables from 10 Monte Carlo simulations under yearly averaged spawning and recruitment, and seasonal spawning and recruitment. Steady-state values are similar, except for higher biomasses of small piscivorous fish and lower biomasses of large piscivorous fish under seasonal reproduction.

2.3 Uncertainty and variability

Real ecological systems are highly variable, and model output is arguably represented most realistically in terms of frequency distributions of potential behaviours (Gardner and O'Neill, 1983; Bar Massada and Carmel, 2008). The shape of distributions of model behaviours will depend on model formulation as well as the distributions of model parameters. Uncertainty regarding model formulation and parameter estimates will translate into variability in model predictions and so comparing distributions of model predictions under differing assumptions can inform understanding of the effects of uncertainty in the modelling process.

Determining the shape of distributions for model parameters in ecological models is troublesome because many ecological processes are difficult to characterise and measure with certainty. Gardner and O'Neill (1983) recommend using triangular distributions for model parameters when detailed information regarding the shape of parameter distributions is unavailable; however the use of 'peaked' distributions requires a range of assumptions regarding the height, width and position of peaks. In CORSET we use the more conservative approach of assuming uniform distributions for parameters, with the minimum and maximum values for each parameter derived from a large body of literature. Any value within a parameter range is equally likely to be selected by the model. This assumption is conservative because it results in greater variation in model outputs than assuming some form of peaked parameter distribution, where the selection of extreme parameter values is less likely than selecting intermediate values.

Given uniform distributions, several options are available for varying parameters within defined ranges in space and time. These options (which represent different model formulations) are:

- (i) Parameter values are reselected at random from defined ranges but are fixed in space and time for each model run
- (ii) Values are reselected at random for each reef cell in each model run but are kept constant across yearly time steps within each run
- (iii) Values are reselected at random at each yearly time step but are fixed across reef cells
- (iv) Values are reselected at random for each reef cell at each yearly time step

Method (iv) was used for sensitivity analyses presented in preceding sections, and for model validation and scenario analyses documented in Chapters 1, 3, 4 and 5. Here we use Monte Carlo simulation to examine variability in steady-state community composition under all four methods of selecting parameter values. Community composition is represented in principal components space.

Steady-state community composition is most variable under parameter selection method (i), and least variable under method (iv) (Figures 2.10 and 2.11). High variability under method (i) is unsurprising as this method chooses single parameter values for an entire run so that dynamic sensitivities associated with selecting atypical parameter settings can be compounded over the course of the simulation period. Interestingly, community composition was more variable under method (iii) where parameters were fixed in time (i.e. for each yearly time step) than under method (ii) where parameters were fixed in space (i.e. for each reef cell). In Figure 2.10, PC1 is an axis of decreasing coral cover, while outlying model runs on the second principal component axis, PC2,

represent community states with particularly high macroalgal cover. These outlying runs with high macroalgal cover are likely to occur under parameter conditions generating low competitiveness of macro turf. These conditions were identified as leading to high macroalgal cover in Section 2.2.

We also examined distributions of model predictions at different spatial scales – local, subregional and regional – under parameter selection method (iv). We used the first principal component, PC1, from principal components analysis of average community composition in the five model sub-regions (Figure 2.1) and community composition in five randomly selected $0.5 \text{ km} \times 0.5 \text{ km}$ reef cells. PC1 captured 47% of the total variance and was an axis of decreasing coral cover. Local-scale community composition was more variable than subregional- and regional-average community composition (Figure 2.12). This result is not surprising (since subregional- and regional-scale community composition is the mean of local-scale values) but it does have implications for making predictions about reef state at local versus subregional and regional scales.

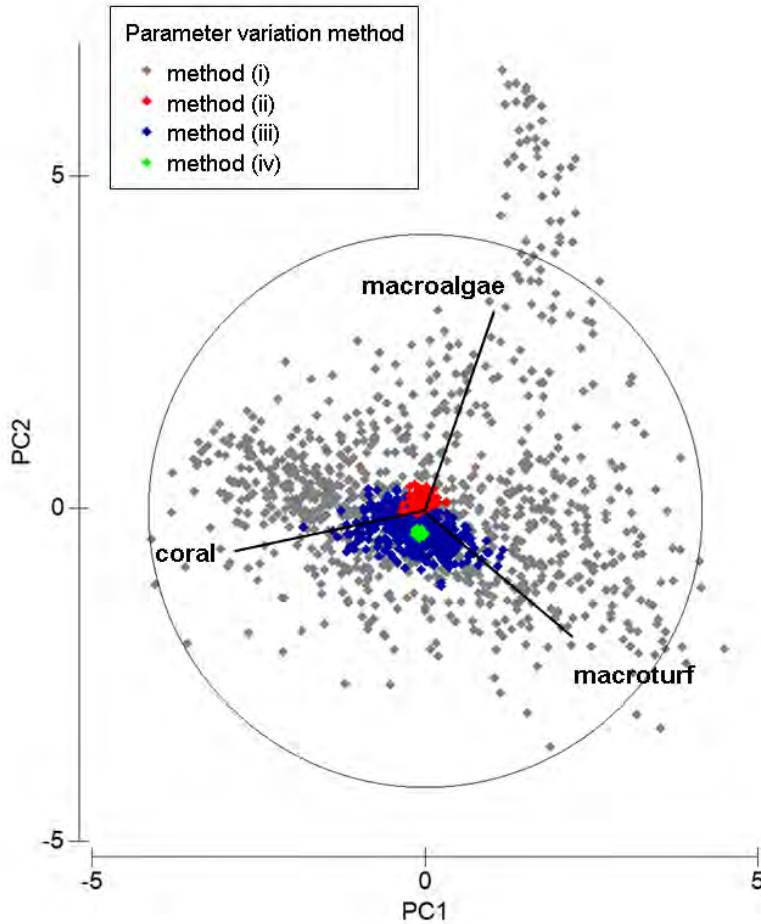


Figure 2.10: Principal components ordination of steady-state community composition from Monte Carlo model runs under different parameter variation methods: (i) variation between model runs (1000 runs); (ii) variation between reef cells (100 runs); (iii) variation between yearly time steps (500 runs); and (iv) variation between cells and between time steps (100 runs). Community composition is more variable under methods (i) and (iii). 41% of the total variance is captured by PC1 (23%) and PC2 (18%).

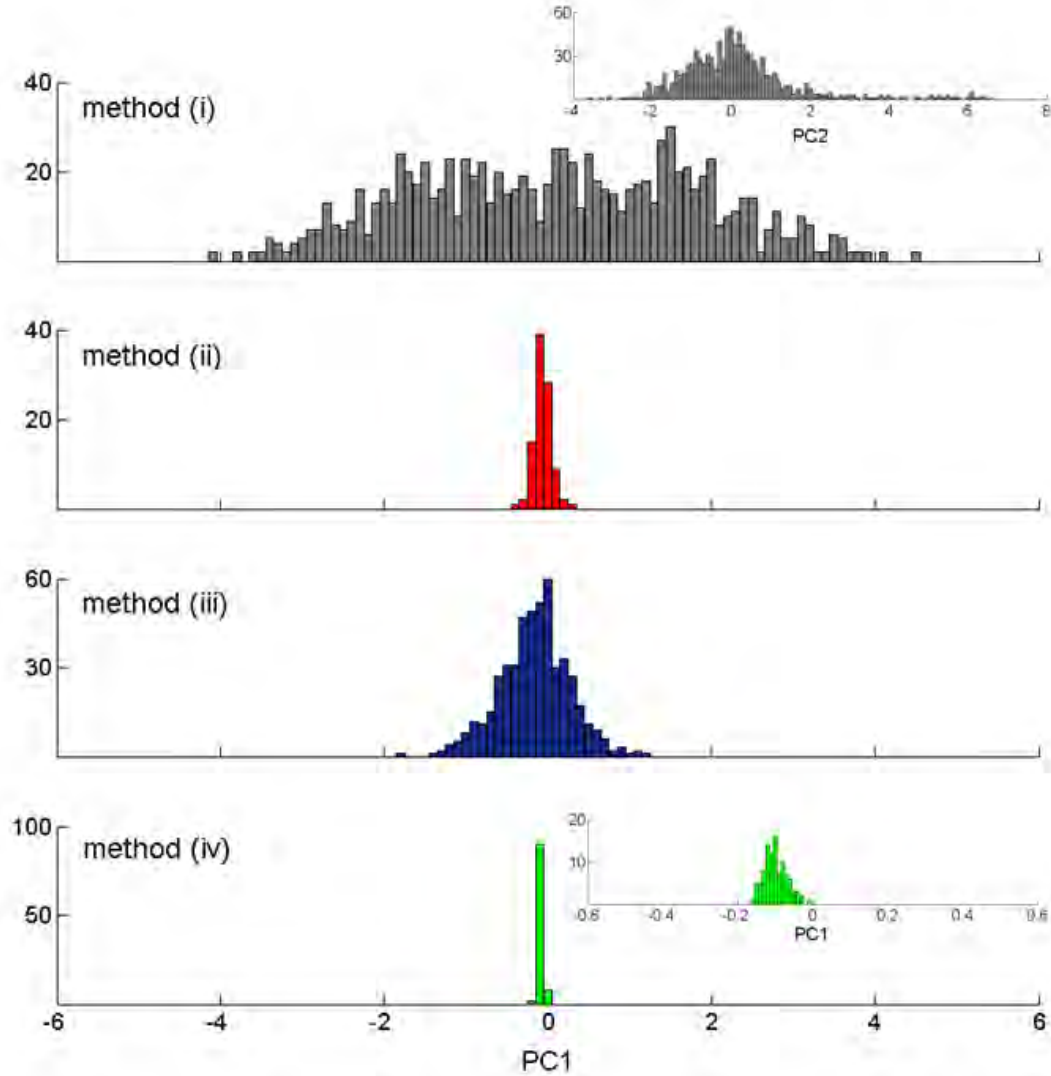


Figure 2.11: Frequency distributions of principal component scores (PC1 from Figure 2.10) for steady-state community composition from Monte Carlo model runs under different parameter variation methods: (i) variation between model runs (1000 runs); (ii) variation between reef cells (100 runs); (iii) variation between yearly time steps (500 runs); and (iv) variation between cells and between time steps (100 runs). Steady-state community composition is more variable under methods (i) and (iii). Inset for method (i) is the frequency distribution of principal component scores on PC2 emphasising left skew of modelled community state on this axis. Inset for method (iv) is the frequency distribution for PC1 using smaller bins.

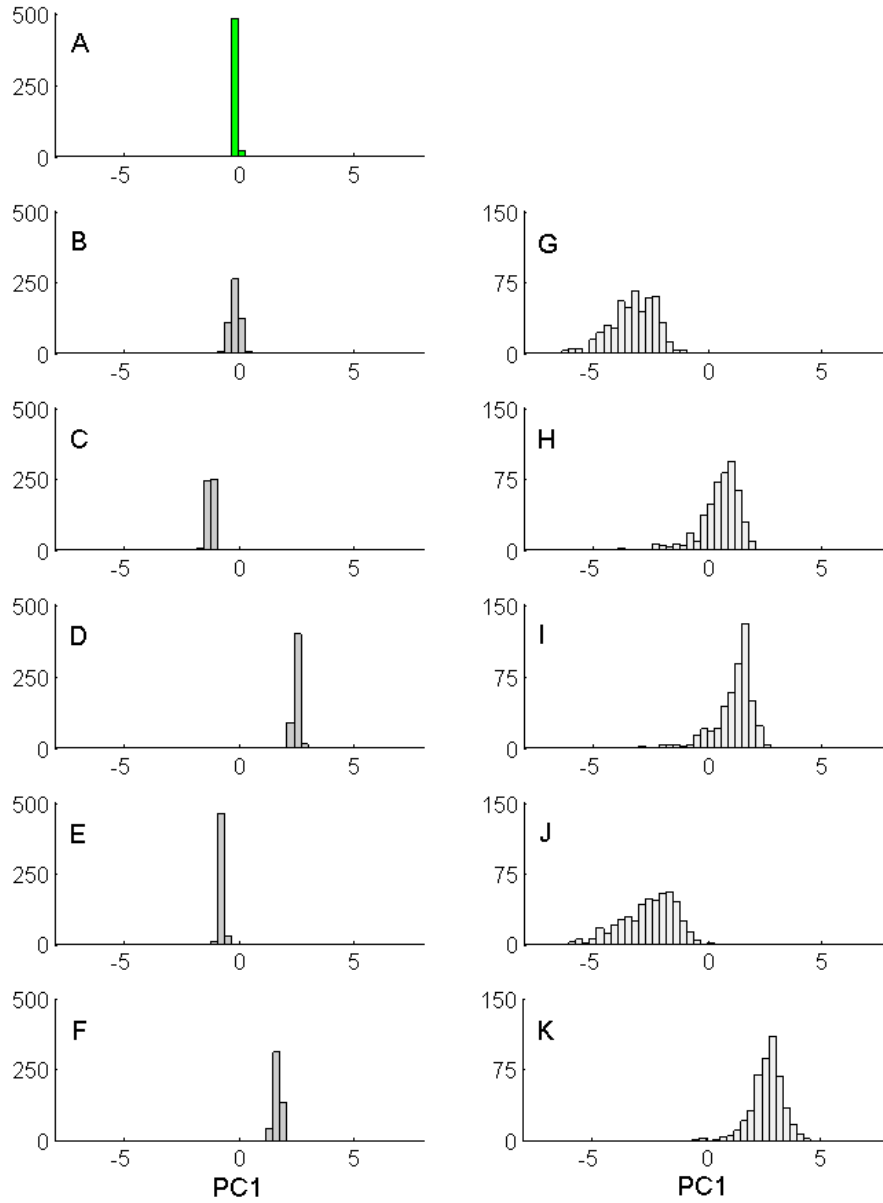


Figure 2.12: Frequency distributions of principal component scores for steady-state community composition at (A) regional, (B – F) subregional, and (G – K) local scales under parameter variation method (iv), i.e. allowing variation in parameter values between reef cells and yearly time steps. PC1 captured 47% of the total variance and was an axis of decreasing coral cover. Regional-scale community composition (A) refers to the average across all reef cells in the model domain while subregional-scale community composition (B – F) refers to averages across reef cells within each of the five subregions identified in Figure 2.1. Local scale distributions (G – K) are derived from five randomly selected $0.5 \text{ km} \times 0.5 \text{ km}$ reef cells. Distributions represent output from 500 Monte Carol model runs. Local-scale community composition is more variable than the regional- and subregional-scale averages.

2.4 Discussion

Characterising model sensitivity and uncertainty is important both in a research context and particularly where models are used in decision support for management. We provide a detailed analysis of sensitivity and uncertainty for a multi-scale model of coral reef dynamics, CORSET, and use multivariate approaches to visualise variability in modelled reef state and reef recovery trajectories. We characterise sensitivity to initial conditions, parameter limits, spatial resolution and temporal resolution (Table 2.2). We also explore the effects of uncertainty about model formulation (in particular different schemes for varying parameters in space and time) on the shape of distributions of model predictions. Our findings have implications for model design and their interpretation can be used to inform management for coral reef systems.

Table 2.2: Summary of sensitivity responses under steady-state conditions and perturbation scenarios.

	Steady-state	Perturbation
Initial conditions	Trajectories converge to steady-state values regardless of initial conditions	Not examined
Parameter limits	Steady-state community composition is sensitive to some model parameters	Varied responses depending on parameter conditions
Spatial resolution	Differences in steady-state community composition are not ecologically significant	Differences in steady-state community composition are not ecologically significant
Temporal resolution	Equivalent steady-state community composition for all updating intervals ≤ 1 fortnight Evidence for sensitivity of community composition to event scheduling	Not examined

Implications for modelling

Sensitivity analysis for coral reef models has generally been confined to examining the sensitivity response of single state variables such as coral cover (e.g. McClanahan, 1995; Mumby, 2006b). Here we show that useful information can be gleaned from exploring multivariate community responses to changes in modelling assumptions. While our analysis of sensitivity and uncertainty is limited to the instantiation of CORSET for the Meso-American Reef system, our findings have broader implications, both for other instantiations of this model and for coral reef modelling in general. For example, the instantiation of CORSET for the Philippines region of the South China Sea (Chapter 4) not only uses the same fundamental model structure, but many of the parameter ranges describing local-scale ecological processes for this region overlap with those for Meso-America (see Table A1, Appendix A). In these circumstances we might expect similarities in sensitivity responses.

The choice of appropriate spatial scales at which to observe and model ecological systems depends on the research or management question, as well as the cost involved with considering regional-scale dynamics at high spatial resolutions. Here we demonstrate that despite what is effectively

cartographic error resulting from the aggregation of reef cells from finer to coarser resolution base maps, differences in regional-scale model behaviour at different spatial resolutions are not ecologically significant (Figure 2.8). However, for a fixed spatial resolution, model behaviour (and hence model predictions of reef community composition) was notably more variable at the local scale than at subregional and regional scales (Figure 2.12). This finding, combined with the fact that parameter estimates are likely to be more uncertain at the local scale, indicates that predictions of reef dynamics at local scales are less robust than those at regional or subregional scales, at least under a mean-field approach such as the one used here.

Variability in model predictions of reef community state also depends on model formulation, in particular different assumptions about parameter variation in space, time and between model runs (Figures 2.10 and 2.11). The choice of an appropriate scheme for modelling parameter variability will in turn depend on the context in which the model is being used and patterns of variability in nature. Fixing parameters across space and allowing variability only between model runs or between time steps (parameter variation methods (i) and (iii) in Section 2.3) is not particularly realistic given spatial variability in ecological processes (e.g. Connell et al., 1997; Dunstan and Johnson, 2005). Nevertheless, these methods give a better representation of the full spectrum of possible model behaviours. We have assumed that spatial and temporal variability in model parameters within runs provides the most realistic representation of real variability in ecological processes, however this assumption significantly damps variability in average model behaviour across runs. Damped variability occurs because each individual model run samples a large portion of the parameter space so that model runs are more similar to each other than in cases where parameters are fixed in space or time for each run. However, information regarding differences in the degree to which particular parameters vary in space and time in particular reef systems is generally unavailable. These questions and assumptions have significant implications for approaches to ecological modelling, but have not generally been considered in models for coral reef systems.

A limitation of our approach to assess sensitivity and uncertainty in CORSET is that we did not explore sensitivity to larval connectivity patterns. Simulated patterns of larval connectivity can be highly sensitive to assumptions about the biological characteristics of marine larvae, for example mortality rates and active swimming (Paris et al., 2007). Furthermore, patterns of larval connectivity in coastal environments have been shown to be highly stochastic (Mitarai et al., 2008; Siegel et al., 2008). The implications of these findings for models of marine ecosystems warrants further investigation. Our exploration of uncertainty arising from alternative model formulations is also limited. While we do examine the effects of incorporating seasonal reproduction and recruitment in CORSET, and in Section 2.3 we explore differing assumptions about the nature of spatio-temporal parameter variability, we have not examined other uncertainties in model formulation. Examples of uncertainties in our model build that are not examined here include the effects of (i) introducing size and age classes for fish and coral functional groups, (ii) allowing movement of fish biomass between cells (in the current version of CORSET we model only reef-associated fish species and assume that there is no movement of fish biomass between reef cells in the order of $0.5 \text{ km} \times 0.5 \text{ km} - 2 \text{ km} \times 2 \text{ km}$), and (iii) including or excluding particular functional groups. This third issue – the inclusion or exclusion of coral reef functional groups – has been explored at the local scale by Fung (2009).

Implications for management

Identifying and communicating sensitivity and uncertainty is critical to the informed and effective application of simulation models in decision support for management. Sensitivity to ecological parameters, if real, can provide important information in terms of managing the impacts of stressors on reefs. In an ecological model for Caribbean fore-reef communities Mumby (2006b) found that coral cover was most sensitive to the level of grazing pressure and, to a limited extent, coral mortality. We found that reef community composition and recovery trajectories following disturbance were particularly sensitive to parameters characterising the life history of corals, namely growth, mortality and fecundity rates. We have reasonable confidence in estimates of coral growth and mortality rates (see Fung, 2009, for detailed derivations), but less confidence in estimates of coral larval production because of a lack of data to parameterise this term, and the fact that larval production was used as a calibration variable (Chapter 1). Coral growth and mortality are themselves sensitive to chronic stressors such as sedimentation and eutrophication, and Carilli et al. (2009a) have shown that local stressors can reduce resilience to coral bleaching through suppression of coral growth rates. In devising management strategies to maintain or improve coral reef resilience, it is important to consider not only the degree of physical stress but the effects of stress on those biological parameters which most influence resilience.

The use of Monte Carlo approaches and probability density functions is well established in ecological risk assessment (e.g. Suter et al., 1987; Rossi et al., 1993; Schobben and Scholten, 1993) but less so in the evaluation of results from simulation models (but see Bar Massada and Carmel, 2008). Examining frequency distributions to characterise variability in model predictions has benefits from both a modelling and management perspective as it effectively communicates the likelihood of particular outcomes as well as the ‘spread’ of potential model behaviours. We advocate more widespread use of probability approaches in communicating model results for decision support, in particular for evaluating the likelihood of different reef futures under alternative management scenarios.

Conclusions

We demonstrate the multi-dimensional nature of variability associated with sensitivity and uncertainty in a complex systems model for coral reefs in the Meso-American region. We use multivariate approaches to characterise sensitivity to parameter values and spatio-temporal resolution under steady-state and perturbed conditions. Our results indicate that modelled reef state and recovery trajectories are particularly sensitive to coral life history parameters, namely growth, mortality and fecundity rates. We show that uncertainty in model formulation – in particular, the way in which ecological processes vary in space and time – has implications for the variability of model outputs. Through comparing distributions of model predictions at different spatial scales we conclude that predictions are likely to be more robust at subregional to regional scales than at the local scale of individual reef cells. The implications of predictability in considering alternative scenarios for coral reef futures are explored in Chapter 3.

Chapter 3

Regional-scale scenario analysis for the Meso-American Reef system: modelling coral reef futures under multiple stressors

Abstract

Coral reefs worldwide are under threat from a wide variety of stressors and disturbances, many of which act in a synergistic manner to affect reef health. The future of coral reef systems at local, regional and global scales is highly uncertain, which poses a challenge to decision makers in designing appropriate strategies for managing human activities that affect reef resilience. Scenario analysis using simulation models can inform decision making by exploring possible futures under alternative management frameworks. Here, we use a spatially explicit, regional-scale simulation model for coral reefs in the Meso-American Reef system to explore the effects of multiple stressors and disturbances on reef state. Two complementary approaches to scenario analysis help to characterise potential reef responses to the combined impacts of climate and land-use change in the Meso-American Reef region. Sedimentation and nutrification emerge as key factors in decreasing the resilience of reef systems to climate change effects. The average community composition of degraded reef systems exposed to high levels of stress and disturbance tends to be more predictable than community composition on reefs that are subject to lower levels of stress and disturbance. This observation applies at both subregional (10^4 – 10^5 m) and regional (10^6 m) scales and reflects a finite bound to the effects of degradation on coral reef communities.

3.1 Introduction

Coral reef ecosystem function is under severe threat from a broad range of chronic stressors and acute disturbances. Of particular concern is the resilience of reef systems to climate change effects, namely coral mortality following bleaching events, reduced coral growth under ocean acidification and potential changes in the frequency and intensity of damaging storms (Emanuel, 2005; Hoegh-Guldberg et al., 2007; Nyberg et al., 2007; Baker et al., 2008; Eakin et al., 2008; Elsner et al., 2008; Veron et al., 2009). There is evidence that chronic local stressors can decrease the resilience of reefs to episodic bleaching events (Carilli et al., 2009a, 2010), and that these chronic stressors often act synergistically to affect reef health (McCook, 1999; McCook et al., 2001; Burkepile and Hay, 2006). Synergies occur where the response to multiple stressors exceeds the sum of responses to individual stressors, i.e. effects are multiplicative rather than additive (McClanahan et al., 2002; Dunne, 2010). Reducing the number of synergistic stressors is an important priority in building resilience to climate change effects, but the nature of synergies is likely to vary between different reef systems and across different spatial and temporal scales.

Models are useful tools for exploring questions regarding synergistic effects and the resilience of coral reef systems (e.g. McCook et al., 2001; Mumby, 2006b; Fung, 2009), and are increasingly used in ‘ecological futures studies’ (Coreau et al., 2009). Ecosystem futures research uses scenario analysis to explore the potential implications of human activities for ecological change (e.g. the Millennium Ecosystem Assessment; MA, 2005). Scenarios are “plausible stories about how the future might unfold” (Biggs et al., 2007). Peterson et al. (2003) and Coreau et al. (2009) distinguish between quantitative and qualitative approaches to scenario analysis. The former are based on predictions from quantitative models, while the latter focus on the development of narratives (e.g. ‘scenario planning’) but can also incorporate predictions from qualitative models. Documented scenario analyses for coral reef systems include both qualitative approaches (e.g. Dambacher et al., 2007; Scopéltis et al., 2007; Bohnet et al., 2008; Bohensky et al., 2009) and quantitative approaches (e.g. McClanahan, 1995; Hoegh-Guldberg et al., 2007; Little et al., 2007; Chang et al., 2008; Donner, 2009). Quantitative scenario analyses have tended to focus on fisheries and on the implications of atmospheric CO₂ concentrations for coral bleaching and ocean acidification. While the importance of multi-scale approaches has been recognised in qualitative scenario planning (Kok et al., 2007), there is a distinct lack of spatially explicit quantitative approaches that consider the interaction of climate change effects with other stressors and disturbances that affect reef state.

Coral reefs are complex, multi-scale and multi-process systems, and past experience demonstrates that the behaviour of reef systems can be difficult to predict (Knowlton, 1992). The future of coral reefs is uncertain, particularly given our lack of knowledge about the combined impacts of multiple stressors in coastal ecosystems (Crain et al., 2009). From a management perspective, it is important to know when and where our predictions about these impacts are likely to be more reliable, and whether predictability can be improved through increased knowledge, i.e.:

- Are reef futures less certain at local, regional or global scales?
- Do we have more confidence in short-term or long-term predictions?
- Do reef dynamics become more or less predictable as systems degrade?

- Are reef systems inherently unpredictable or is there scope to improve our predictions of reef dynamics through increased knowledge of fundamental processes?

Here, we use a spatially explicit simulation model – CORSET (Coral Reef Scenario Evaluation Tool; Melbourne-Thomas et al., 2010, in press) – to examine the potential implications of multiple, uncertain stressors for the future of the Meso-American Reef system (MAR).

The MAR extends over 1000 km from the northern tip of Mexico’s Yucatan Peninsula to the Bay Islands in Honduras (Figure 3.1). The region is subject to a range of anthropogenic threats, in particular the southward expansion of coastal development along the Mexican coast, increasing pressure from tourism in Belize, and the impacts of sedimentation from coastal run-off in Honduras (Arrivillaga and Garcia, 2004). Uncertainty regarding reef futures in the MAR stems from a range of factors, in particular:

- (i) Limited understanding of groundwater transport of pollutants to coastal reefs in Mexico and northern Belize. Waste water and sewage from resorts and urban areas are generally untreated (Murray, 2007), and the highly porous karst geology of this region is likely to facilitate transport of liquid wastes from inland to coastal areas (Perry et al., 2009). However this connection is not well understood and groundwater management in the region is limited.
- (ii) Limited information regarding the potential impacts of climate change on marine systems in the region. Existing studies are non-predictive (e.g. Halpern et al., 2008) or focus on potential impacts on terrestrial systems (Anderson et al., 2008a). Potential climate change effects in the MAR that will have consequences for coral reef function include increased sea surface temperatures (which will increase the risk of coral bleaching), ocean acidification, increased intensity of damaging storms, and changes in precipitation. Precipitation influences sediment inputs to coastal areas, particularly in Honduras where several major rivers deposit terrestrially derived sediments at the coast (Thattai et al., 2003; Burke and Sugg, 2006). Increased terrestrial run-off in Honduras has potential implications for other reef locations in the MAR through ocean transport of suspended matter (Chérubin et al., 2008; Paris and Chérubin, 2008).

We use two complementary approaches to modelling reef futures in the MAR under multiple, uncertain impacts. In the first approach we conduct a broadly scoped ‘scenario sweep’ to gauge system responses to the combined effects of fishing, hurricanes, coral bleaching, nutrification and sedimentation. In our second approach we adopt concepts from the scenario planning literature (Peterson et al., 2003; Bohensky et al., 2006; Bohnet et al., 2008; Bohensky et al., 2009) to model reef futures under spatially explicit scenarios of high-impact, high-uncertainty stressors and disturbances associated with land-use and climate change. We show that modelled reef state tends to be less variable under high levels of degradation and that, beyond a certain point, there is limited scope for degraded reefs to respond to additional impacts. By comparison, there is a much greater range of potential states for modelled reef systems under relatively low levels of stress and disturbance, so that community composition is less predictable when impact levels are low. Our exploration of uncertainty about the future of coral reefs under varying levels of stress and disturbance complements findings from Chapter 2 regarding the effects of uncertainty in the formulation of CORSET on model behaviour.

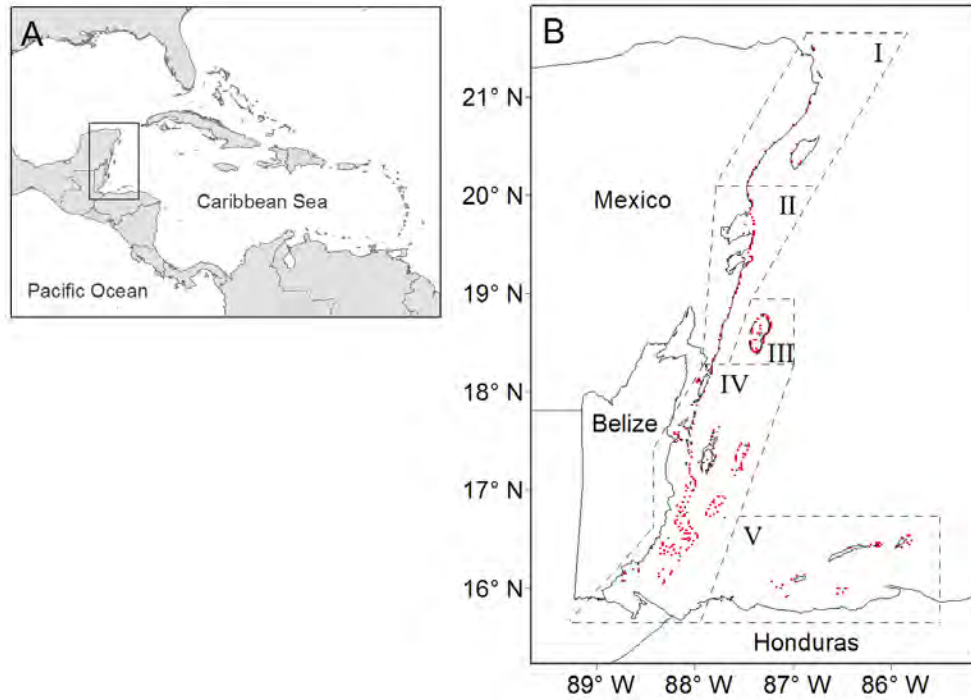


Figure 3.1: Spatial extent of the modelled region; the Meso-American Reef system (MAR). Reef cell locations (indicated in red) were extracted from reef distribution maps from the University of South Florida's Institute for Marine Remote Sensing Millennium Coral Reef Mapping Project (IMaRS, 2004). Areas delineated by dashed lines indicate the extent of the five model subregions (I, II, III, IV & V) which correspond with eco-regional planning units for the MAR (Kramer and Kramer, 2002). Model output presented for subregional scales refers to averages over cells in each of the subregions I–V, while 'regional average' model output is the average over all reef cells in the model domain.

3.2 The model: CORSET

CORSET is a spatially explicit simulation model that couples ecological dynamics from local scales (10^2 m) to regional scales (10^6 m) through ocean transport of larvae. Chapter 1 provides full details of the model formulation; only a cursory description of the main components is provided here. The model simulates proportional covers of five benthic functional groups and biomasses of four functional groups of consumers (see Table 1.1, Chapter 1):

- (i) Benthic groups are made up of spawning and brooding corals (together referred to as 'corals'), macroturf, macroalgae and grazed epilithic algal communities (EAC).
- (ii) Consumer groups consist of herbivorous fish, small-to-intermediate and large piscivorous fish (together referred to as 'piscivores'), and herbivorous sea urchins.

Interactions between these groups are modelled using difference equations (see Appendix A) that are updated on a weekly time step in each $2 \text{ km} \times 2 \text{ km}$ reef cell of a gridded base-map (Figure 3.1).

Parameters that describe local-scale ecological processes are selected at random from predefined ranges that are derived from empirical observations. Parameter values vary between simulation years and between reef cells so that CORSET is stochastic. Transport of coral, fish and sea urchin larvae between reef cells is modelled using connectivity matrices that contain transition probabilities between all source and sink locations in the model domain. These transition probabilities are derived from sophisticated particle tracking simulations that incorporate both hydrodynamic processes and larval behaviour (Paris et al., 2007). Stresses and disturbances are represented as forcing parameters (Table 3.1) that act at local, subregional and regional scales.

Table 3.1: Implementation of forcings in CORSET.

Forcing	Implementation
Fishing pressure	Fishing pressure is defined using published values of total fish catch in the MAR region ^(a,b) and for Caribbean reefs more generally ^(c) and is modelled as a direct decrease in fish biomass. This decrease is apportioned between herbivorous, small-to-intermediate piscivorous and large piscivorous fish groups. Higher fishing pressure on herbivorous fish is assumed for the MAR since piscivorous fish stocks in the region are depleted ^(d) .
Hurricanes	Hurricanes ^(e) are modelled as a decrease in coral cover by a factor of 0.002–0.7 ^(f,g,h,i,j) , and a decrease in macroalgal cover by a factor of 0.9 ^(k) . More severe hurricanes affect a greater proportion of reef cells than lower intensity hurricanes ^(h) . Category 4 and 5 hurricanes are assumed to affect all cells within a reef tract (or subregion), category 3 hurricanes affect two thirds of cells, and category 1 and 2 hurricanes affect one third of reef cells. The location of reef cells affected by category 1, 2 and 3 hurricanes is chosen at random.
Coral bleaching	Coral bleaching events decrease coral cover in the model and the severity of particular events (i.e. the magnitude of the decrease in cover) is derived from the literature. Bleaching events that do not cause coral mortality are not modelled.
Nutrification	Nutrification ^(l) increases macroalgal growth by a factor of 2–7 ^(m,n,o,p,q) and decreases coral larval production by a factor of 0–0.25 ^(r,s) .
Sedimentation	Sedimentation increases coral mortality by 0–0.2 yr ⁻¹ ^(t) , decreases survival of coral recruits by a factor of 0.6 ^(u) and prevents recruitment of coral onto macro turf ^(v) .

^(a)Koslow et al. (1994) ^(b)Arias-González et al. (2004) ^(c)Halls et al. (2002) ^(d)García-Salgado et al. (2006) ^(e)Hurricanes are tropical cyclones with maximum sustained wind speeds ≥ 33 m/s (Nyberg et al., 2007), ^(f)Bythell et al. (1993), ^(g)Cheal et al. (2002), ^(h)Gardner et al. (2005), ⁽ⁱ⁾Lirman (2003), ^(j)Wantiez et al. (2006), ^(k)Mumby et al. (2006), ^(l)*sensu* Szmant (2002) ^(m)Lapointe (1989), ⁽ⁿ⁾Lapointe and O’Connell (1989), ^(o)Larned and Stimson (1996), ^(p)Larned (1998), ^(q)Schaffelke and Klumpp (1998), ^(r)Loya et al. (2004), ^(s)Ward and Harrison (2000), ^(t)Nugues and Roberts (2003), ^(u)Babcock and Smith (2000), ^(v)Birrell et al. (2005).

3.3 Scenario sweep

To gauge model behaviour and potential reef futures under a range of forcing conditions, and to characterise interactions between multiple impacts, we conducted a ‘scenario sweep’ for 32 different combinations of fishing pressure, nutrification, sedimentation, hurricane disturbance and elevated coral mortality associated with bleaching (Table 3.2). Low impact and high impact values were assigned for each forcing and each combination of impacts was examined in a Monte Carlo simulation of 10 model runs of 100 years each. 10 model runs was taken as sufficient because model validation (Chapter 1) and sensitivity analyses (Chapter 2) indicate that variability in model output between runs is small when parameter values are allowed to vary randomly between reef cells and between yearly time steps within each run (which is the approach used here). Low- and high-impacts are assumed to reflect best- and worst-case scenarios for the MAR subject to particular forcings. In Section 3.4 we explore spatially realistic future scenarios for the region under a subset of forcings.

Table 3.2: Details of forcing conditions used in the scenario sweep.

		Low impact	High impact
Fishing pressure ^(a)	(F)	Between zero and the minimum reported value for the region ($0 - 0.08 \text{ g m}^{-2} \text{ yr}^{-1}$)	Between zero and the maximum reported value for the region ($0 - 5.0 \text{ g m}^{-2} \text{ yr}^{-1}$)
Hurricanes	(H)	Hurricane events occur with a long term frequency of once every 20 years (the strength of individual events is randomly determined)	Hurricane events occur with a long term frequency of once every 5 years (the strength of individual events is randomly determined)
Coral bleaching	(B)	Coral bleaching events occur with a long term frequency of once every 20 years	Coral bleaching events occur with a long term frequency of once every 5 years
Nutrification	(N)	No reef cells affected	30% of randomly selected reef cells affected
Sedimentation	(S)	No reef cells affected	30% of randomly selected reef cells affected

^(a)Minimum reported value from Koslow et al. (1994), maximum reported value from Halls et al. (2002).

Fishing pressure for particular reef cells was selected randomly from the defined ranges (Table 3.2) assuming a uniform distribution, and was allowed to vary between years and model runs. Selection of MAR-wide hurricane frequencies is problematic because reported average frequencies for the Caribbean refer to particular sites (Gardner et al., 2005), with a frequency of one event every 10 years considered as high (Mumby et al., 2006). We assumed a low hurricane frequency of once every 20 years and a high frequency of once every 5 years for the MAR. These events affected a proportion of cells in a random number of randomly selected subregions. High frequency of severe coral bleaching events (once every 5 years) was derived from Donner et al. (2005) and Donner (2009). Coral bleaching once every 20 years as a low-impact frequency is conservative. Coral mortality due to bleaching was assumed to be between 0.2–60%, where 60% is the maximum mortality reported for the region following the severe 1998 bleaching event (Kramer and Kramer, 2000). As for hurricane events, each modelled bleaching event affected a random number of (randomly selected)

subregions in the MAR. Because the scenario sweep is not intended to be spatially realistic, but rather to provide an overview of model behaviour and potential reef futures under multiple impacts, we did not include spatial preferences for fishing activity or differential susceptibilities of particular reef cells or subregions to coral bleaching and hurricanes.

Comparing end points

We used multivariate approaches (PERMANOVA, PERMDISP, constrained and unconstrained ordination; Anderson et al., 2008b) to characterise differences in modelled community composition after 100 years from the scenario sweep. PERMANOVA detects differences in multivariate location and dispersion (i.e. the ‘spread’ of observations in multivariate space) and can accommodate complex designs such as the one used here with 5 main effects and 26 interaction terms. PERMDISP tests for homogeneity of multivariate dispersion between groups; it does not test for interaction effects. All multivariate analyses were conducted using normalised reef state data as the units for benthic state variables (%) and consumer state variables (g/m^2) differ.

We distinguish between three cases within the combined PERMANOVA/PERMDISP analyses of scenario sweep end-points (Table 3.3):

- (i) Main effects which show significant differences in dispersion (F, H and S).
- (ii) Interaction effects which are significant in the PERMANOVA, but for which there is no significant difference in dispersion between levels (e.g. $H \times N$).
- (iii) Interaction effects which show significant differences in both PERMANOVA and PERMDISP analyses (e.g. $F \times H$).

Interpretation of case (i) effects is appropriate if patterns of dispersion are consistent between main effects and grouped interaction terms. For example, if dispersion is greater at high-impact and low-impact levels for two given main effects (e.g. F_{high} and H_{low}), then dispersion should also be greater under the high-low level when these two terms are combined, i.e. higher dispersion for the group $F_{\text{high}}H_{\text{low}}$ than for the groups $F_{\text{high}}H_{\text{high}}$, $F_{\text{low}}H_{\text{high}}$ and $F_{\text{low}}H_{\text{low}}$. This pattern holds for all but one set of grouped terms ($B \times S$) for which there was no detectable difference in dispersion (Figure 3.2). Interpretation of significant 2-way interactions – cases (ii) and (iii) – is appropriate because dispersion patterns for the 4-way interaction term ($F \times H \times B \times S$) were consistent with dispersion patterns for the main and 2-way effects, i.e. dispersion was highest under $F_{\text{high}}H_{\text{low}}B_{\text{low}}S_{\text{low}}$. Case (ii) enables examination of the nature of interactive (and potentially synergistic) effects between forcings that manifest as differences in the location of multivariate means in PERMANOVA. These differences in location are confounded by differences in dispersion under case (iii). We therefore examine cases (i) and (ii) (Figures 3.3 and 3.4).

Table 3.3: Summary of PERMANOVA and PERMDISP results from the scenario sweep. Forcing effects are abbreviated as F (fishing), H (hurricanes), B (bleaching), N (nutrification) and S (sedimentation). The response is reef community composition (regional average) after 100 years. Only main effects and significant interactions from the PERMANOVA are presented (assuming $\alpha=0.05$). Analyses were conducted using normalised data and Euclidean distances. PERMDISP results for interaction effects refer to differences in dispersion between group levels (e.g. for $F \times H$, there is a significant difference in dispersion between the four groups $F_{\text{high}}H_{\text{high}}$, $F_{\text{high}}H_{\text{low}}$, $F_{\text{low}}H_{\text{high}}$ and $F_{\text{low}}H_{\text{low}}$). Significant P(permutation) values from PERMDISP analyses (assuming $\alpha=0.05$) are asterisked. These values have not been adjusted for inflated Type I error. 9999 permutations were used for PERMANOVA (permutation of residuals under a reduced model) and PERMDISP.

Effect	PERMANOVA			PERMDISP		
	df	Pseudo-F	P(permutation)	df	F	P(permutation)
F	1	150.2	0.0001	1	10.07	0.0048*
H	1	118.3	0.0001	1	11.02	0.0029*
B	1	79.77	0.0001	1	1.850	0.2032
N	1	31.93	0.0001	1	3.640	0.0738
S	1	180.0	0.0001	1	4.473	0.0406*
$F \times H$	1	6.185	0.0003	3	9.265	0.0002*
$F \times B$	1	9.801	0.0001	3	9.326	0.0003*
$F \times N$	1	6.461	0.0002	3	4.815	0.0095*
$F \times S$	1	19.41	0.0001	3	16.85	0.0001*
$H \times B$	1	3.139	0.0195	3	4.659	0.0055*
$H \times N$	1	6.496	0.0002	3	2.999	0.0518
$H \times S$	1	7.287	0.0001	3	1.781	0.1732
$B \times S$	1	16.94	0.0001	3	1.282	0.3028
$N \times S$	1	2.648	0.0389	3	4.163	0.0087*
$F \times H \times B \times S$	1	2.928	0.0243	15	4.811	0.0001*

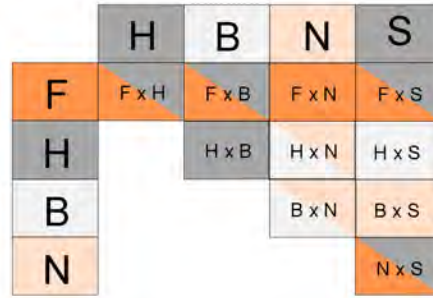


Figure 3.2: Graphical summary of dispersion patterns from the scenario sweep. Orange boxes indicate cases where average dispersion was greatest under the ‘high impact’ level of a particular forcing (e.g. greater dispersion under F_{high}), while grey boxes indicate cases where average dispersion was greatest under the ‘low impact’ level of a particular forcing (e.g. greater dispersion under H_{low}). Boxes for interaction effects (e.g. $F \times H$) are shaded to indicate the levels for grouped forcings with the greatest average dispersion. For example, of the four groups within the $F \times H$ interaction ($F_{\text{high}}H_{\text{high}}$, $F_{\text{high}}H_{\text{low}}$, $F_{\text{low}}H_{\text{high}}$, $F_{\text{low}}H_{\text{low}}$), dispersion was greatest at high fishing impact and low hurricane frequency ($F_{\text{high}}H_{\text{low}}$), which is consistent with dispersion patterns for the main effects. Lighter-shaded boxes indicate non-significant PERMDISP results. Dispersion patterns are consistent between main effects and interaction terms in all cases except for $B \times S$, for which PERMDISP was non-significant. Dispersion patterns for the 4-way interaction term ($F \times H \times B \times S$) are not represented here but were consistent with dispersion patterns for main effects, i.e. dispersion was highest under $F_{\text{high}}H_{\text{low}}B_{\text{low}}S_{\text{low}}$.

Different levels of fishing (F), hurricanes (H) and sedimentation (S) effects were associated with significant differences in the dispersion of community structure and so are classified as case (i). Dispersion is well represented by distance preserving (unconstrained) ordination. We therefore used non-metric multi-dimensional scaling (MDS; Clarke, 1993) to visualise differences in dispersion under high- and low-impact treatments for fishing, hurricanes and sedimentation (Figure 3.3). Community composition is more dispersed under high fishing pressure, low hurricane frequency and low sedimentation. Modelled reef community composition under high fishing pressure is characterised by high macro turf and macroalgal cover, while reefs under high hurricane frequency are characterised by high macro turf and EAC cover (which is unsurprising given that hurricanes reduce both macroalgal and coral cover). Under high sedimentation, modelled reef state is characterised by high macro turf cover.

Dispersion patterns in model outcomes can be interpreted in terms of the predictability of future reef states; greater dispersion in modelled reef state over multiple model runs implies lower predictability. Our results indicate that, when considered in isolation, forcings that remove fish biomass decrease the predictability of future reef states, while forcings that decrease coral cover (sedimentation and hurricanes) translate into a marginal increase in predictability. This pattern arises because under high fishing pressure, chance events can precipitate crashes in fish stocks. Thus, crashes happen in some model runs but not others and we see greater variability between

model runs under high fishing pressure. In contrast, decreases in coral cover caused by chronic stress or periodic disturbance generate a degraded reef state that has a low probability of recovery, particularly if the level of stress or frequency of disturbance is high. We therefore see lower variability between model runs under high sedimentation and high hurricane frequency, reflecting that degraded reefs converge on a community composition where algal cover is high, and where coral cover and the biomass of all fish groups is low.

We used canonical analysis of principal components (CAP; Anderson et al., 2008b) to visualise 2-way interaction effects under case (ii), namely $H \times S$, $B \times S$ and $H \times N$. These interactions were significant in the PERMANOVA of scenario sweep end-points (Table 3.3) but there were no differences in dispersion between combined treatment levels (non-significant PERMDISP results). CAP is a constrained ordination technique that discriminates between *a priori* groups; in this case it is equivalent to classical canonical discriminant analysis because we used Euclidean distance as the the resemblance measure. Treatment levels that represent combined high-impact forcings under case (ii) (e.g. $H_{\text{high}}S_{\text{high}}$) are consistently characterised by high macro turf cover, while modelled coral communities under combined low-impact forcings (e.g. $H_{\text{low}}S_{\text{low}}$) are characterised by high coral cover and fish biomasses (Figure 3.4).

If stressors and disturbances act synergistically to affect reef state, i.e. the combined effect is greater than the sum of individual effects, we would expect the multivariate distance between low-low \rightarrow high-high levels of combined forcings to exceed the sum of low-low \rightarrow low-high and low-low \rightarrow high-low distances. This is not the case for any of the 2-way interactions shown in Figure 3.4. In all three cases the combined effect of forcings is less than the sum of individual effects, where effect size is interpreted as the average multivariate distance between groups. Hence, hurricane, bleaching, sedimentation and nutrification forcings as modelled here can be interpreted as high-magnitude, limited-scope forcings. Each individual forcing results in such a degraded reef state that the presence of another forcing has limited scope to produce further degradation. We call this kind of interaction ‘preemptive effects’; the presence of one high impact forcing preempts the effect of additional forcings. There is evidence for preemptive effects for all the 2-way interactions listed in Table 3.3 but, with the exception of the three cases presented in Figure 3.4, differences in multivariate location between groups are confounded by differences in dispersion.

Temporal and spatial variability

We used the best- and worst-case scenarios (all forcings at low impact and all forcings at high impact, respectively) from the scenario sweep to examine temporal and spatial variability in model outcomes. MDS ordination of regional-average community composition, used here to capture variability in reef state over time, indicates a clear divergence in trajectories under best- and worst-case scenarios (Figure 3.5). Under the best-case scenario, the average model trajectory over 100 years occupies the portion of MDS space associated with high coral cover and fish biomass. In contrast, modelled reef state under the worst-case scenario tends towards low coral cover and fish biomass. Variability in end-points (between model runs) is associated with differences in the levels of macroalgal cover and sea urchin biomass for both the best- and worst-case scenarios. The outlying end point under the worst-case scenario in Figure 3.5 represents a model run in which the number of hurricane events was anomalously low. Since macroalgal cover is reduced by hurricanes

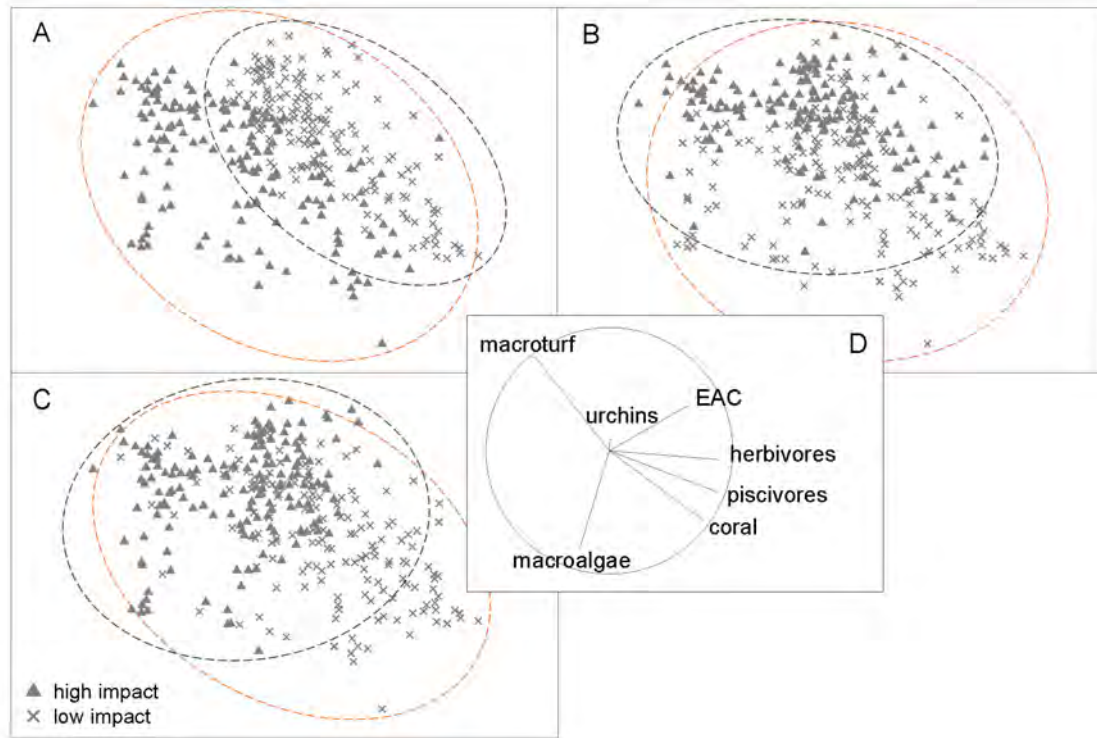


Figure 3.3: MDS ordinations of modelled community state (normalised regional averages) after 100 years under 32 scenarios (10 Monte Carlo model runs each). 2D stress = 0.14. Ellipses identify differences in dispersion between high and low impact scenarios for (A) fishing, (B) hurricanes and (C) sedimentation. Community composition is more dispersed under high fishing, low hurricane frequency and low sedimentation (orange ellipses) than under low fishing, high hurricane frequency and high sedimentation (black ellipses). Probability values from PERMDISP analyses are provided in Table 3.3. (D) indicates vectors of Pearson correlations between functional groups (i.e. state variables) and the ordination axes. Grazed epilithic algal communities are abbreviated as ‘EAC’.

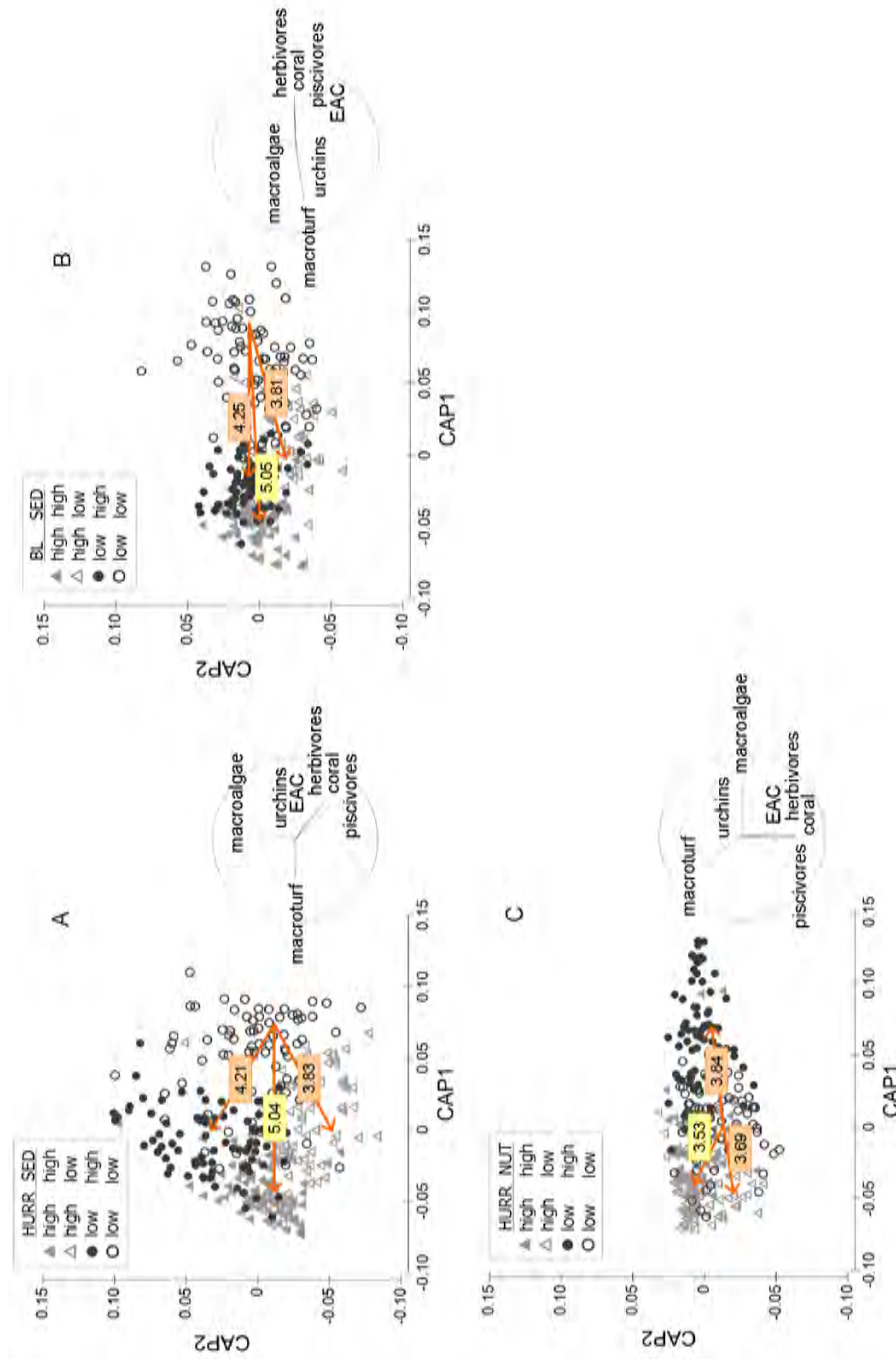


Figure 3.4: Two-way CAP ordinations of modelled community state (normalised regional averages) after 100 years under 32 scenarios (10 Monte Carlo model runs each). Ordinations are constrained by levels of 2-way interactions between (A) hurricanes \times sedimentation, (B) bleaching \times sedimentation and (C) hurricanes \times nutrification. Orange arrows represent average Euclidean distances between groups. Values for these distances are overlaid in orange for distances between low and medium levels of total impact (i.e. from the case where both impacts are low to the case where just one impact is high), and in yellow for the distance between lowest and highest total impact. Values indicated in yellow are less than the sum of values indicated in orange, which is evidence for 'preemptive effects'. Pearson correlations between functional groups (i.e. state variables) and the ordination axes in (A), (B) and (C) indicate that modelled communities are characterised by high macrobenthos cover in cases where both impacts are high (filled grey triangles), and by high coral cover and fish biomasses where combined impacts are low (open circles).

in the model (Table 3.1), the chance eventuality of a low number of hurricane events over 100 years in the worst-case scenario results in anomalously high macroalgal cover. In model runs with high macroalgal cover sea urchins may benefit from the increased availability of algae for grazing. However, the actual magnitude of variability in urchin biomass across runs is relatively low in this case (in the order of 0.5 g/m^2), and the association between macroalgal cover and urchin biomass does not hold at the subregional scale (Figure 3.6).

Spatial variability in modelled reef state after 100 years also differs between the best- and worst-case scenarios (Figure 3.6). Variability in community composition between subregions was greater under the best-case scenario than under the worst-case scenario (see Figure 3.1 for subregion delineations). Under heavy pressure from stressors and disturbances reef state tends to become uniformly degraded across space so that subregional differences in modelled reef assemblages disappear. As for the regional scale, variation in community composition for degraded reefs at the subregional scale is associated with differences in macroalgal cover (Figure 3.6E). For the best-case scenario, variability in modelled community composition within and between subregions is associated with differences in the covers and biomasses of all functional groups.

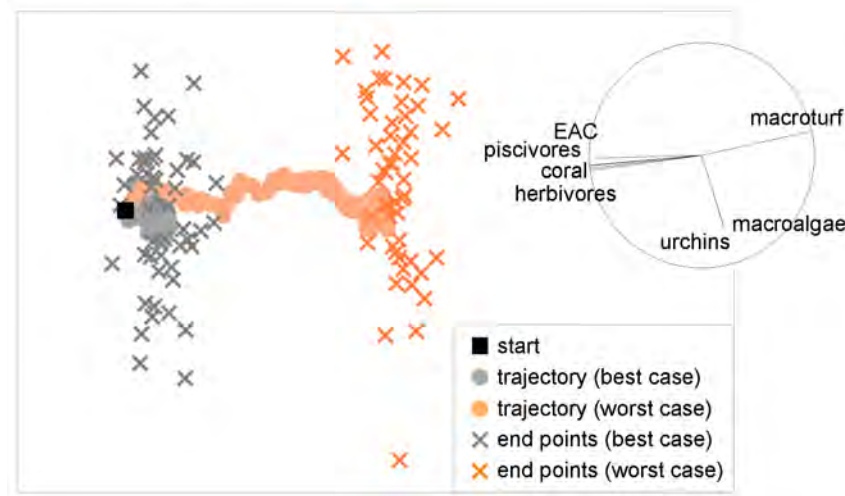


Figure 3.5: MDS ordination of model trajectories over 100 years for the best-case (grey) and worst-case (orange) scenarios from the scenario sweep. 2D stress = 0.08. Ordinated points represent normalised yearly averages of multivariate community state for the MAR region. Grey and orange circles are means from 50 model runs, while crosses indicate community composition after 100 years for each of 50 model runs. Pearson correlations between functional groups (state variables) and the ordination axes indicate that variability in end points under both the best- and worst-case scenarios is associated with differences in levels of macroalgal cover and sea urchin biomass. There is no significant difference in dispersion between end points under the best- and worst-case scenarios; $P(\text{perm}) = 0.054$.

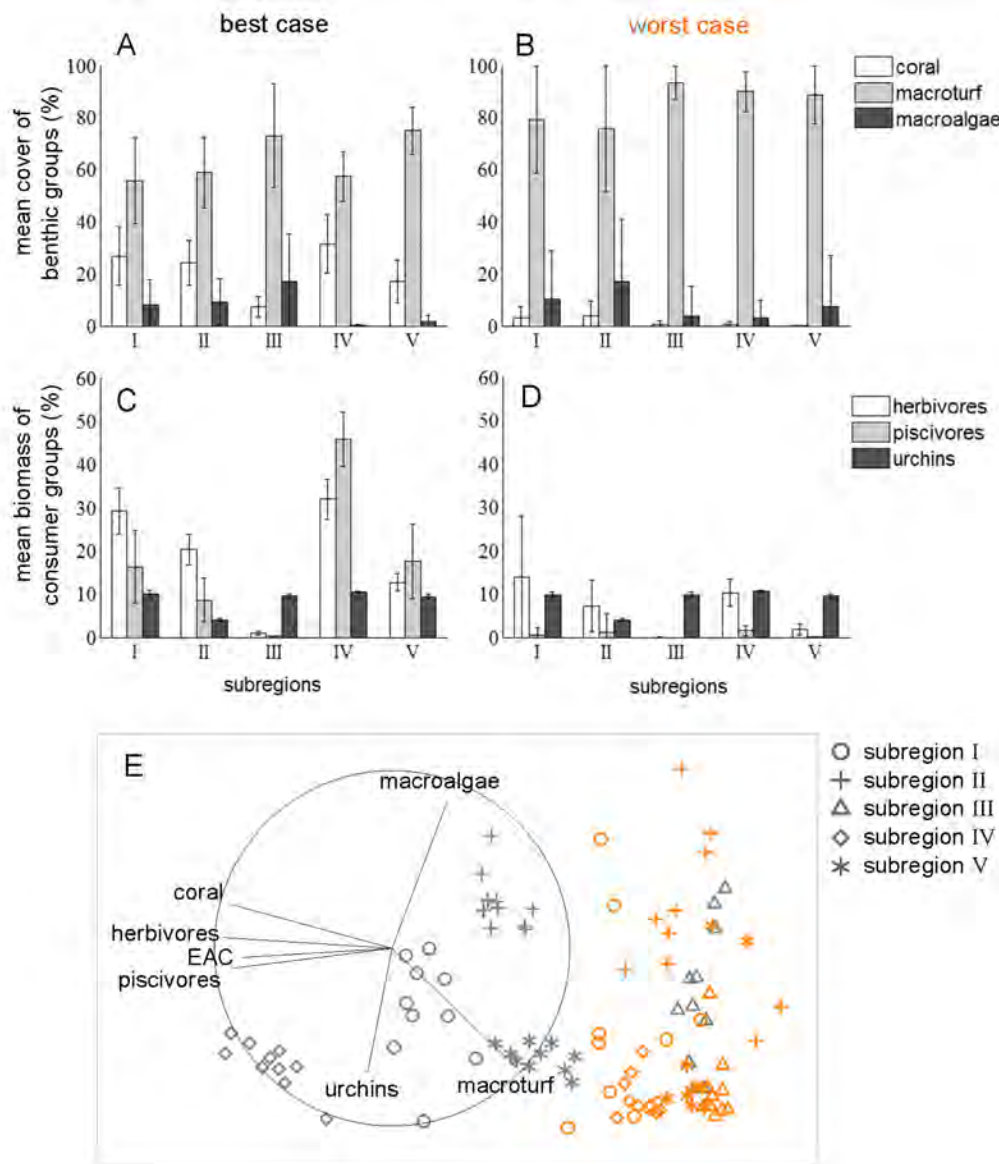


Figure 3.6: Spatial variability in reef community composition after 100 years under the best- and worst-case scenarios from the scenario sweep. Average values across subregions for individual functional groups are given in (A)–(D). (A) and (C) show benthic and consumer group means and 95% confidence intervals from 10 model runs in each of the five subregions under the best-case scenario (all forcings at low impact). (B) and (D) show subregional means for the worst-case scenario (all forcings at high impact). In (E), reef community composition is ordinated in MDS space (2D Stress = 0.1), with vectors of Pearson correlations between functional groups and ordination axes overlaid. Reef state under the best-case scenario (grey) is significantly more dispersed than under the worst-case scenario (orange); $P(\text{perm}) = 0.0002$.

3.4 Reef futures under land-use and climate change

Bohnet et al. (2008) and Bohensky et al. (2009) present an approach to qualitative scenario analysis (for the Great Barrier Reef region and sustainable ecotourism in Papua New Guinea, respectively) which considers factors affecting the future which have both high impact and high uncertainty in terms of when, where and how impacts might affect social-ecological systems. In both studies, high-impact, high-uncertainty factors were elicited from stakeholders, and scenarios under different levels of these factors were explored in a workshop setting. Here, we use a similar approach to scenario analysis for coral reefs in the MAR region, but with high-impact, high-uncertainty factors derived from the scenario sweep and based on knowledge gaps in the literature. Results from the scenario sweep indicate that four model forcings – hurricanes, bleaching, sedimentation and nutrification – had a high impact on reef state, and interacted as ‘preemptive effects’ (Figure 3.4). The individual and combined effects of these forcings on future reef state in the MAR is uncertain.

We used two axes to define our scenario space (Figure 3.7). One describes uncertainty regarding potential changes in land-use practices in the region (which captures sedimentation and nutrification impacts), and the other describes uncertainty in climate change impacts (which captures hurricane and coral bleaching impacts). The quadrants defined by these axes represent four alternative future scenarios: (i) regulated land-use change and ‘best-case’ climate change impacts, (ii) unregulated land-use change and ‘best-case’ climate change impacts, (iii) regulated land-use change and ‘worst-case’ climate change impacts, and (iv) unregulated land-use change and ‘worst-case’ climate change impacts. We explored reef futures under these scenarios over a period of 100 years. In reality our axes describe continuous variation in the degree of impact, but here we chose four spatially realistic and distinct scenarios to demonstrate the use of CORSET in scenario analysis for the MAR.

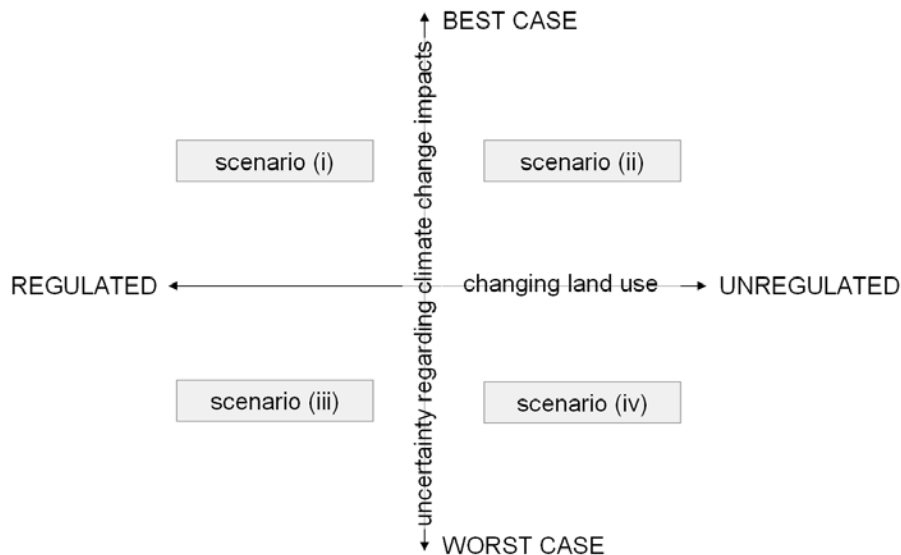


Figure 3.7: Reef future scenario axes for land-use and climate change (based on scenario planning approaches from Bohnet et al., 2008 and Bohensky et al., 2009).

We use the term ‘land-use change’ to refer to both increasing coastal development (particularly hotel building and urban development) and increasing agricultural activity leading to increased sediments and nutrients in coastal run-off. The spatial distribution of these impacts was derived from Burke et al.’s (2004) Reefs at Risk in the Caribbean analysis (coastal development and sedimentation risk categories). Regulated land-use change involves management measures such as enforcement of a particular level of waste-water treatment and measures to minimise agricultural run-off. Under these conditions we assume that all high-risk reef locations from Burke et al.’s (2004) analysis are affected by nutrification and sedimentation, and that with unregulated land-use change there is an additional increase over time in the number of medium- and low-risk reef locations affected by nutrification and sedimentation. We did not include sediment and nutrient transport dynamics in our scenarios, but Burke et al.’s (2004) risk estimates include a proxy for sediment dispersion from river mouths.

Under the ‘best-case’ scenarios for climate change impacts we assumed coral bleaching mortality to occur with a long-term frequency of once a decade (following Donner et al., 2005 and Donner, 2009), and hurricanes (categories 1–5) to occur with a long-term frequency of once every 20 years. There is limited information regarding spatial variation in bleaching susceptibility in the MAR, particularly for predictions into the future. Coral mortality was highest in Belize and Honduras following the severe 1998 bleaching event, which could have been associated with greater thermal stress in the southern MAR. However, it is likely that patterns of bleaching mortality in 1998 were confounded with the spatially variable effects of Hurricane Mitch (Kramer and Kramer, 2000). We modelled bleaching in the MAR as coral mortality events, with each event affecting reef cells in a random number of subregions. We assumed coral bleaching mortality to be between 0.2–60%, as for the 1998 event (Kramer and Kramer, 2000).

Under the ‘worst-case’ scenarios for climate change impacts we assumed coral bleaching mortality to occur with a long-term frequency of once every 5 years (again following Donner et al., 2005 and Donner, 2009) and hurricanes (categories 3–5) to occur with a long-term frequency of once every 20 years. Our assumption of increased hurricane intensity is in keeping with the most recent predictions for changes in Atlantic hurricane activity over the 21st century under anthropogenic warming (Bender et al., 2010). Note that for our worst-case climate change scenarios we used conservative estimates for frequencies of coral bleaching and hurricanes. These frequencies differ from impact levels used in the scenario sweep (Table 3.3), which was designed to gauge reef behaviour at the extremes of possible forcing values. We excluded the potential effects of ocean acidification on coral growth rates in scenarios (i)–(iv), as projections for the responses of reef builders to increasing dissolved CO₂ are as yet too uncertain (Anthony et al., 2008). Fishing pressure was within the range 0–5 g m⁻² yr⁻¹ (Halls et al., 2002) for all four scenarios.

We examined differences in modelled community composition from 50 Monte Carlo model runs under scenarios (i)–(iv). Results are presented for regional and subregional scales at 25, 50 and 100 years into the future (Figures 3.8 and 3.9). Average community composition at the regional scale differed significantly between scenarios after 25 years, and this difference persisted to 50 and 100 years (Table 3.4). There was a significant difference in dispersion between scenarios at 50 and 100 years, but not at 25 years. Reef community composition was less dispersed under scenarios (ii) and (iv) – the unregulated land-use scenarios – at 50 and 100 years (Figure 3.8).

At the subregional scale, PERMANOVA detected significant scenario \times subregion interactions after 25, 50 and 100 years, which were associated with significant differences in dispersion between grouped interaction levels (Table 3.4). Despite apparent interactions, modelled community composition under scenarios (ii) and (iv) was consistently less dispersed than under scenarios (i) and (iii) at the subregional scale (average dispersion values for individual scenarios at the subregional scale are not reported). Reduced dispersion at regional and subregional scales under scenarios (ii) and (iv), i.e. under unregulated land-use, is consistent with reduced dispersion under high sedimentation observed in the scenario sweep. Highly degraded reefs converge to an algal-dominated state that has a very low probability of recovery and so model outcomes are less dispersed over multiple runs.

There were distinct differences in modelled community state between subregions at 25, 50 and 100 years (which are visualised in multivariate space in Figure 3.9), but these differences were less pronounced after 100 years. Subregion III was typified by higher macroturf and macroalgal cover, and lower coral cover and fish biomass than other subregions. Reefs in subregion III were identified as vulnerable to disturbance in Chapter 1, reflecting inherently low larval supply to this subregion. Subregions I, II, IV and V were distinguished from each other by the relative dominance of macroalgae and macroturf, with reefs in subregions II and V generally characterised by higher macroalgal cover than reefs in subregions I and IV. Variability between model runs within subregions I, II, IV and V occurred along a gradient of coral cover and fish biomass, i.e. from a ‘healthy’ state under scenario (i) to a highly degraded state under scenario (iv).

Table 3.4: Summary of PERMANOVA and PERMDISP results from the four reef future scenarios for land-use and climate change. The response is reef community composition (regional and subregional averages) after 25, 50 and 100 years. Analyses were conducted separately for each level of ‘Year’ (i.e. 25, 50 and 100 years) using normalised data and Euclidean distances. P(permutation) values from PERMDISP analyses have not been adjusted for inflated Type I error. 9999 permutations were used for PERMANOVA (permutation of residuals under a reduced model) and PERMDISP.

Scale	Year	Effect	df	PERMANOVA		PERMDISP	
				Pseudo-F	P(permutation)	F	P(permutation)
Region	25	scenario	3	12.35	0.0001	2.540	0.0796
	50	scenario	3	26.34	0.0001	6.165	0.0009
	100	scenario	3	58.34	0.0001	11.18	0.0001
Subregion	25	scenario	3	48.82	0.0001	10.40	0.0001
		subregion	4	397.8	0.0001	6.201	0.0001
		scen \times subreg	12	2.647	0.0001	3.210	0.0001
	50	scenario	3	90.10	0.0001	42.13	0.0001
		subregion	4	296.1	0.0001	17.01	0.0001
		scen \times subreg	12	6.811	0.0001	9.573	0.0001
	100	scenario	3	190.1	0.0001	95.28	0.0001
		subregion	4	252.3	0.0001	15.82	0.0001
		scen \times subreg	12	19.34	0.0001	14.96	0.0001

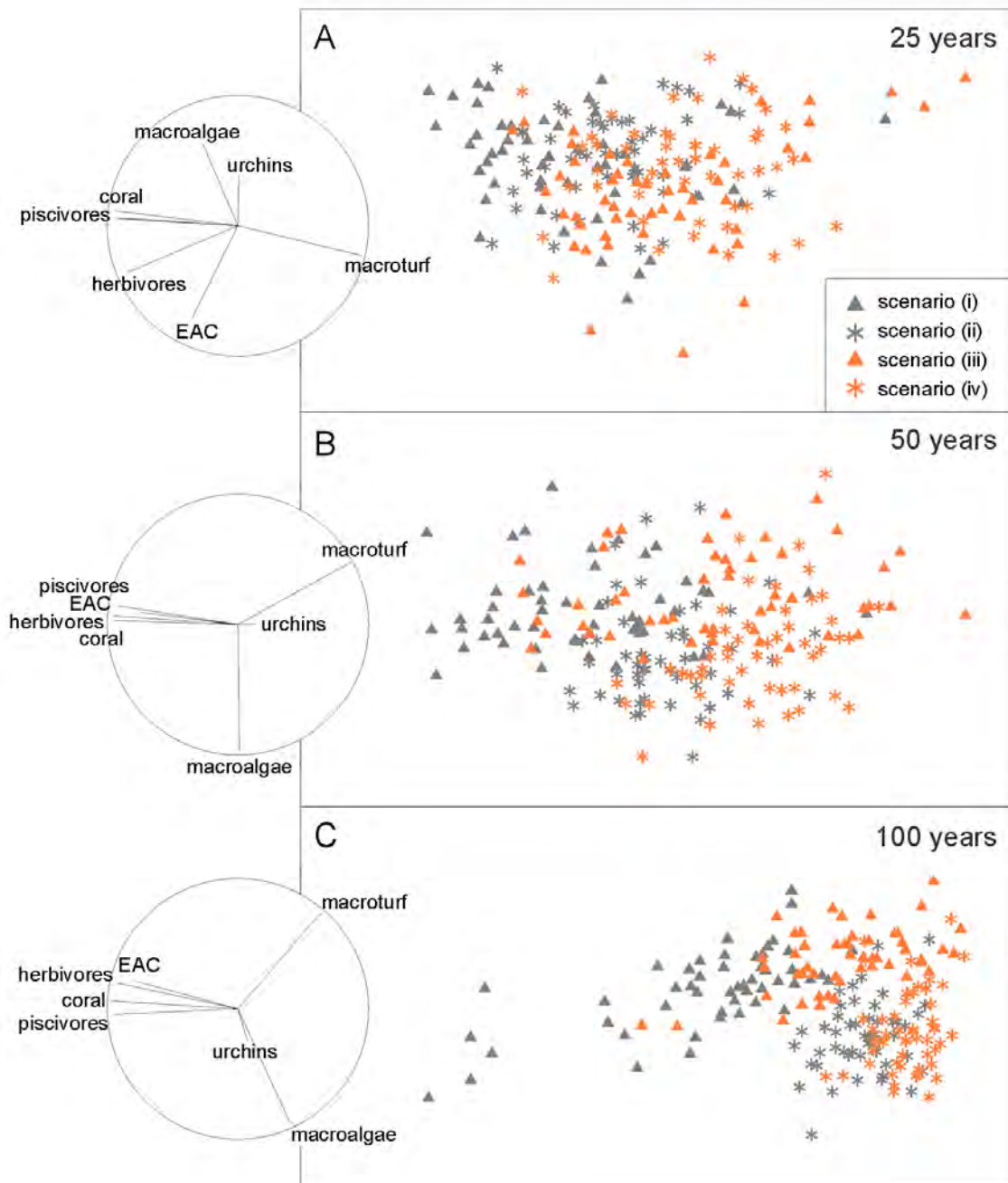


Figure 3.8: MDS ordinations of modelled community state (normalised regional averages) after (A) 25 years, (B) 50 years and (C) 100 years under four future scenarios (50 Monte Carlo model runs each). Vector overlays of Pearson correlations between functional groups and ordination axes give an indication of differences in community composition between scenarios. Scenario (i) is typified by higher fish biomass and coral cover, while scenarios (ii)–(iv) are characterised by high macro turf and macroalgal covers. In (B) and (C) there is a significant difference in dispersion between scenarios (see Table 3.4). Scenarios (ii) and (iv) are less dispersed than scenarios (i) and (iii). 2D Stress = 0.14 (A), 0.12 (B) and 0.10 (C).

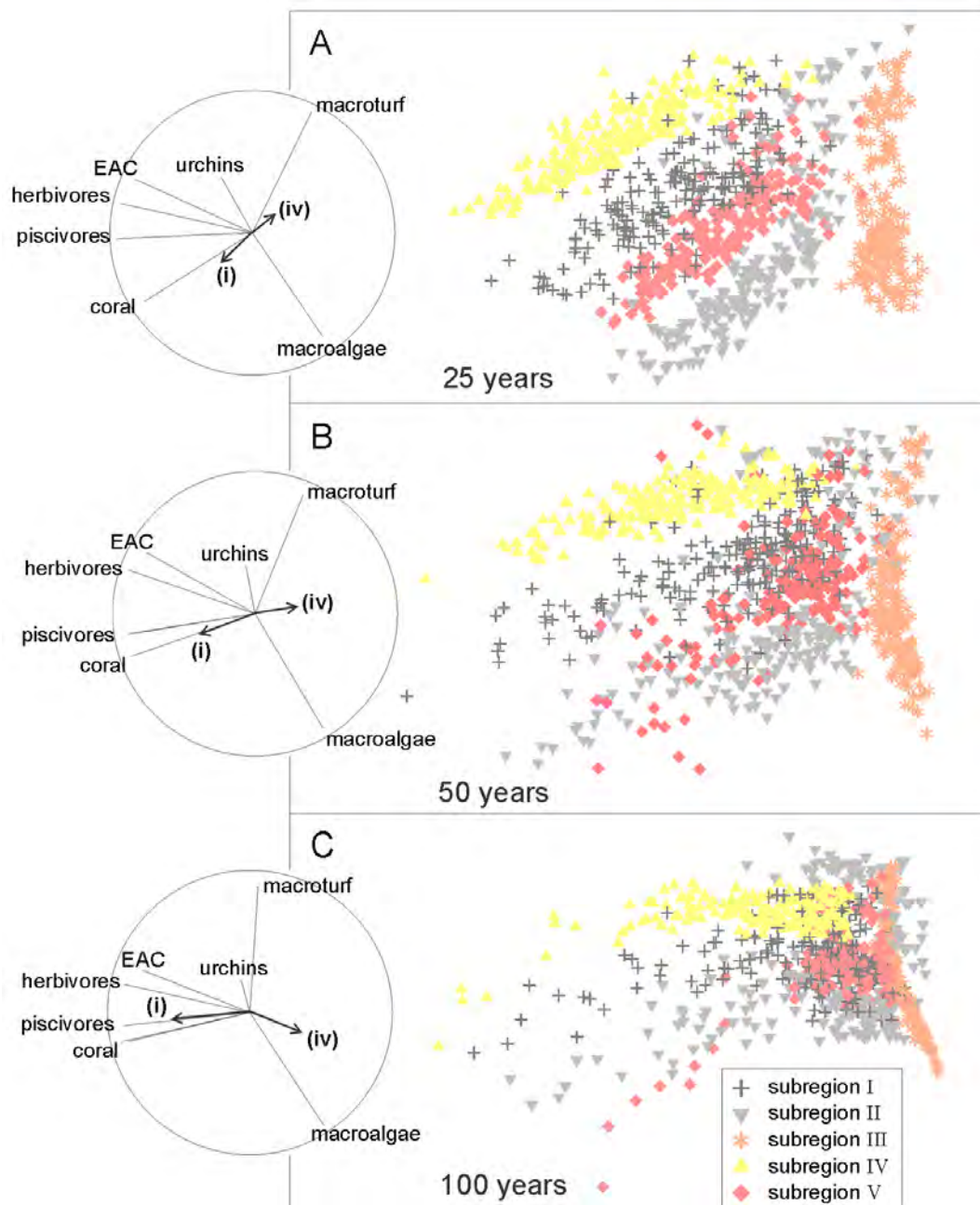


Figure 3.9: MDS ordinations of modelled community state (subregional averages) after (A) 25 years, (B) 50 years and (C) 100 years under four future scenarios (50 Monte Carlo model runs each). Vector overlays of Pearson correlations between functional groups and ordination axes give an indication of differences in community composition within and between subregions. Scenarios (i) and (iv) are included in vector overlays to indicate directionality in the change in community composition from the best case (regulated land-use and low climate change impacts) to the worst case (unregulated land-use and high climate change impacts). Subregion III is characterised by higher macro turf and macroalgal covers, and lower coral cover and fish biomass than other subregions. Subregions I, II, IV and V are distinguished from each other by the relative dominance of macroalgae and macro turf, while variability between model runs for each of these subregions occurs along a gradient of coral cover and fish biomass. Reefs are generally characterised by higher coral cover and fish biomass under scenario (i) compared with scenario (iv). 2D Stress = 0.14 (A and B) and 0.13 (C).

We used modelled coral cover to calculate subregional Reef Health Index values (according to threshold values defined in the Healthy Reefs Initiative Eco-health Report Card for the Mesoamerican Reef; HRI, 2008) at 25, 50 and 100 years under the four future scenarios (Figure 3.10). Widespread, regional-scale degradation was apparent after 50 years under both scenarios for worst-case climate change (scenarios (iii) and (iv)), and reefs in all subregions were degraded to a ‘Critical’ level (<5% coral cover) after 100 years under scenarios (ii), (iii) and (iv). Loss of coral cover was most significant in subregions III and V, and losses were most pronounced under scenario (iv) – combined impacts of land-use and climate change. Given that our worst-case climate change scenarios are reasonably conservative, it is likely that the timescale for loss of coral cover in the MAR in the future will be smaller than our predictions.

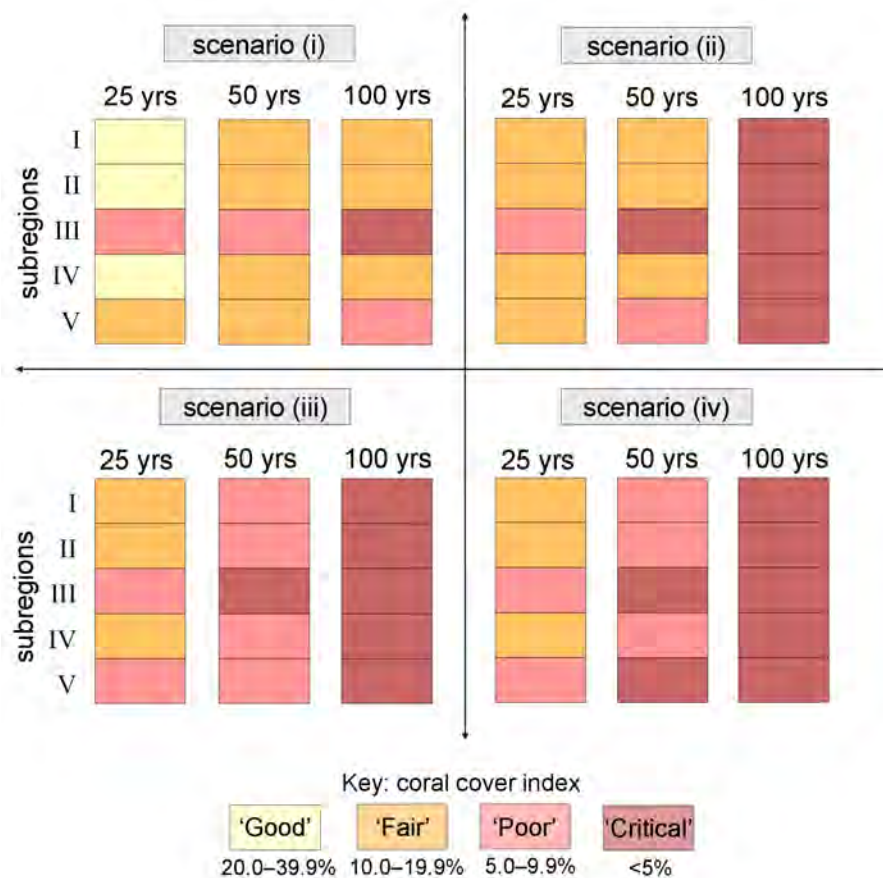


Figure 3.10: Average Reef Health Index categories from modelled coral cover (using threshold values from HRI, 2008) under the four future scenarios: (i) regulated land-use change and best-case climate change impacts, (ii) unregulated land-use change and best-case climate change impacts, (iii) regulated land-use change and worst-case climate change impacts, and (iv) unregulated land-use change and worst-case climate change impacts. Index categories are colour coded; yellow = ‘Good’ (20.0–39.9% coral cover), orange = ‘Fair’ (10.0–19.9%), light red = ‘Poor’ (5.0–9.9%) and dark red = ‘Critical’ (<5%), and are presented for each of the five MAR subregions at 25, 50 and 100 years into the future.

3.5 Discussion

We present results from two complementary approaches to scenario analysis using a spatially explicit simulation model (CORSET) for coral reefs in the MAR region: (i) a broad scenario sweep to gauge responses to forcings that represent the impacts of five key stressors and disturbances for reefs in the region; and (ii) four spatially realistic scenarios that examine reef futures under high-impact, high-uncertainty forcings. Our findings have implications for understanding the potential effects of multiple stressors on reef state and the predictability of community composition under alternative future scenarios.

Reef futures under multiple stressors

A major cause of reef degradation worldwide is the combined effect of multiple stressors (McClanahan et al., 2002; Veron et al., 2009). Various authors have described synergistic effects of multiple stressors on reef function (e.g. McCook, 1999; McCook et al., 2001; Anthony et al., 2008). However, Dunne (2010) documents multiple cases of misuse of the term ‘synergy’ in the coral reef literature and emphasises the distinction between statistically significant interactions that represent synergistic (amplification of an additive effect) and antagonistic (reduction in an additive effect) responses. While the preemptive effects we identify in Section 3.3 are strictly antagonisms, we distinguish them here because we do not interpret these interactions as cases of “active opposition” (Concise Oxford English Dictionary) between effects. Instead, the system itself has limited scope for response under combined forcings, i.e. a badly degraded reef has limited scope to degrade further in response to new, additional stressors. Darling et al. (2010) document a similar effect of combined stressors in the form of fishing and coral bleaching over a 20-year period on Kenyan coral reefs. The effect of both stressors on coral cover is described by these authors as antagonistic or weakly additive and they cite the dominant effect of coral bleaching as a possible reason for the lack of a synergistic response. We suggest that the underlying mechanism behind this observation may be similar to the preemptive effects identified using CORSET.

We observed preemptive effects between (i) hurricanes and nutrification, (ii) hurricanes and sedimentation, and (iii) bleaching and sedimentation over long time scales of 100 years. This timescale is clearly outside the scope of observational studies. However, limited reef recovery following hurricane and bleaching events has been documented over decadal time series (Gardner et al., 2005; Baker et al., 2008), and the effect of terrestrial run-off has been correlated with reduced coral resilience to bleaching (using sclerochronologies) over century-scale time series (Carilli et al., 2010). In our spatially realistic scenarios for land-use and climate change, the rate of reef degradation was reduced under lower nutrification and sedimentation. Importantly, reduction of terrestrial run-off is a possible management lever in the MAR. Management actions could include replanting mangroves to trap sediment, maintaining vegetative barriers along waterways, and building terraces to reduce soil erosion (Carilli et al., 2009b). Given evidence for subregional- to regional-scale river-reef connectivity in the MAR (Chérubin et al., 2008; Paris and Chérubin, 2008), management of terrestrial run-off is a key priority for building reef resilience in the region.

Predictability of reef futures

Differences in the predictability of future reef states clearly have important implications for decision-making in coral reef management. Here we use the dispersion of model predictions in multivariate space (i.e. variability in predicted community structure) to make inferences about the predictability of modelled reef state under different conditions. Dispersion in reef state tended to be lower for degraded systems characterised by high algal cover, low coral cover and low fish biomasses. While we found some variability within the degraded state in terms of macroalgal cover (Figures 3.5 and 3.6), there was much greater scope for variability in modelled community composition for less degraded reefs in terms of differing levels of coral cover and the biomasses of fish functional groups. For example, low hurricane frequency and low sedimentation impact treatments in the scenario sweep resulted in increased dispersion of modelled community composition (Figure 3.3). In our four scenarios for land-use and climate change, we saw increased dispersion in community composition at regional and subregional scales under regulated land-use scenarios where the impacts of nutrification and sedimentation were low. This result could potentially be interpreted as enhanced adaptive capacity of reef communities to climate change effects when multiple stressors are managed at subregional and regional scales. However, the relationship between predictability of modelled reef states and adaptive capacity requires further examination beyond the scope of this study.

The trend of reduced variability under high impacts of stressors and disturbances contrasts with previous findings for coral reef systems. Warwick and Clarke (1993) document increased variability in coral communities affected by coral bleaching and in reef fish communities under coral mining impacts. However, their findings apply over short time scales and the authors note that increased variability reflected shifts in species assemblages, rather than changes in the abundance of species which were present prior to disturbance. CORSET is not able to capture shifts in species assemblages within functional groups. The fact that our model predictions are less variable under degraded conditions argues against inherent unpredictability in the response of reef systems to stress and disturbance. However, the sequence of disturbances in real reef system (e.g. sequential bleaching or hurricane events) and the degree of impacts from chronic stressors will have a strong effect on the rate of degradation and on the level of recovery between successive disturbance events.

Limitations

Our exploration of possible futures for the MAR necessarily involves simplifications and assumptions. We have endeavoured to be explicit in stating our assumptions. Scenarios for climate and land-use change presented here are reasonably conservative and we did not model potential effects of ocean acidification on coral growth rates or potential increases in fishing pressure. These assumptions enable us to better interpret the combined effects of a subset of uncertain factors that will influence reef state in the future. A more general assumption in using models for scenario analysis is that current relationships hold across time; Carpenter (2002) and Coreau et al. (2009) emphasise that models calibrated on past and/or present data may be poorly adapted to study the future. However, an advantage of CORSET in this respect is that we have not used a model fitting approach but rather a bottom-up approach based on the representation of ecological processes (see Chapter 1 and Fung, 2009). We have reasonable confidence that these processes are applicable for

future projections. Coreau et al. (2009) highlight that “future scenarios are not expected to be validated *ex post*, because they are not expected to predict what will happen, but to explore the wide array of possibilities for the future”.

A further limitation of our approach is that we have not examined management strategies *per se* or their potential effectiveness in increasing reef resilience, rather we have provided a broad assessment of possible reef futures under different conditions. CORSET will be made available via a web portal so users can access the model directly and explore more specific management questions related to, for example, the spatial and temporal scales over which management actions are likely to be most effective. The model will be most effective as a decision support tool when used in combination with other spatial and economic planning tools for reef systems (e.g. Westmacott and Rijsberman, 1995; Watts et al., 2009). We also note that our biophysical approach to modelling coral reef dynamics does not capture the complex feedbacks between ecological and socioeconomic dynamics. Such feedbacks have important consequences for coral reef systems, some of which are explored in Chapter 5.

Conclusions

We demonstrate the use of a spatially explicit simulation model to explore a range of coral reef future scenarios for the MAR. We combine quantitative modelling with approaches from qualitative scenario planning to provide insights into the predictability of future reef states under multiple stressors and disturbances. Our results demonstrate how the effects of stressors and disturbances on modelled reef systems can be ‘preemptive’ such that badly degraded reefs have limited scope to degrade further in response to new, additional stressors. The community composition for these degraded reefs tends to be more predictable than that for ‘healthy’ reefs that have lower algal cover and higher coral cover and fish biomass. Reefs that are subject to fewer chronic stressors are not only more resilient to disturbance but may also have enhanced adaptive capacity by virtue of the fact that they have greater inherent variability.

Chapter 4

A multi-scale biophysical model to inform regional management of coral reefs in the western Philippines and South China Sea

Abstract

The health and functioning of coral reef ecosystems worldwide is in decline, and in the face of increasing anthropogenic stress, the rate of decline of these important ecosystems is set to accelerate. Mitigation strategies at regional scales are costly, but nevertheless critical, as reef systems are highly connected across regions by ocean transport of both larval propagules and pollutants. It is essential that these strategies are informed by sound science, but the inherent complexity of coral reef systems confers significant challenges for scientists and managers. Models are useful tools for dealing with complexity and can inform decision making for coral reef management. We develop a spatially explicit biophysical model for a general coral reef system. The model couples dynamics from local (10^2 m) to regional (10^6 m) scales, and explicitly incorporates larval connectivity patterns derived from sophisticated larval dispersal models. Here, we instantiate and validate the model for coral reefs in the Philippines region of the South China Sea. We demonstrate how the model can be used in decision support for coral reef management by presenting two examples of regional-scale scenario projection relating to key management issues in the Philippines: (i) marine reserve design and the recovery of fish stocks; and (ii) synergistic effects between coral bleaching and poor water quality. These scenarios highlight the importance of considering multiple stressors to reef health and patterns of larval connectivity in regional-scale management decisions.

4.1 Introduction

Models of complex coral reef systems

Coral reefs provide essential ecosystem services to millions of people in coastal populations worldwide (Done et al., 1996; Moberg and Folke, 1999) and the demand for decision support tools to inform the management of these ecosystems is increasing. Coral reefs are inherently very complex, multi-scale and multi-process systems (Hatcher, 1997; Hughes et al., 2005; Dizon and Yap, 2006), the behaviour of which is difficult to understand and predict. Conceptual models, analytical models and simulation models are effective tools to capture some of this complexity and to assess trade-offs that arise in the exploitation and protection of coral reef systems (Van Kouwen et al., 2008). However, ecosystem models for coral reefs have tended to focus on local-scale processes (e.g. McClanahan, 1992, 1995; McCook et al., 2001; Mumby, 2006b; Mumby et al., 2006; Holmes and Johnstone, 2010, but see Gribble, 2003), despite that reefs are highly connected at regional scales by ocean currents, social structures and regional economies.

Ocean circulation and particle tracking models have dramatically improved understanding of dispersal processes for the larvae of coral reef organisms (e.g. James et al., 2002; Paris et al., 2005, 2007; Bode et al., 2006; Cowen et al., 2006), terrestrially-derived suspended particles (Chérubin et al., 2008; Paris and Chérubin, 2008) and contaminants in coastal waters (Condie et al., 2005; Suh, 2006). Predictions from these models have important implications for management, for example in assessing likely recovery trajectories of damaged reef localities. Cowen et al. (2000, 2006) and Paris et al. (2007) demonstrate the importance of considering both circulation patterns and larval behaviour (e.g. vertical migration and attraction towards settlement habitats) in estimating connectivity strengths for coral reef organisms. However there have been limited attempts to incorporate connectivity information derived from sophisticated particle tracking simulations – that include both hydrodynamics and larval behaviour – into ecosystem models (Gray et al., 2006; Little et al., 2007).

We present a spatially explicit regional-scale model of a coral reef system; CORSET (Coral Reef Scenario Evaluation Tool). CORSET captures multi-scale processes by coupling a local-scale ecosystem dynamic model to the regional scale via inter-reef connectivities for coral, fish and sea urchin larvae. Our approach is generic and portable, so that the model can be transferred between global regions. The Meso-American Reef system was used as a test case for CORSET, and validation of the model in this region has been achieved (Melbourne-Thomas et al., in press). Here, we assess the portability of the model by instantiating and validating it for reefs in the Philippines region of the South China Sea.

The Philippines context

The Philippines has one of the most extensive and biodiverse coral reef systems in the world (Gomez et al., 1994; Wilkinson, 2004). Philippine reefs comprise 26% of total reef area in the Southeast Asian region (Burke et al., 2002), and are considered to be the global center of marine fish biodiversity (Carpenter and Springer, 2005). A large coastal population, rapid population growth and high poverty rates have resulted in over-exploitation of Philippine reef fisheries, and

destructive fishing has contributed significantly to reef degradation (Chou, 1998; Licuanan and Gomez, 2000). Offshore reefs in the South China Sea have been the focus of territorial disputes and many of the claims by China, the Philippines, Vietnam and Malaysia are overlapping. Evidence suggests that Philippine reefs in this area – namely the Kalayaan Island Group (Figure 4.1) – may act as larval sources for ‘mainland’ reefs (McManus, 1995). Destruction of reef habitats in the Kalayaan Island Group may therefore have flow-on effects for biodiversity and reef functioning at a regional scale. Controversies over ownership have prevented long-term monitoring of reef condition on offshore reefs in the South China Sea, and uncoordinated enforcement implies susceptibility to unsustainable commercial fishing and destructive fishing practices (Burke et al., 2002).

More generally, three key concerns for coral reef management in the Philippines are overfishing, water quality and threats associated with climate change (Burke et al., 2002; Peñaflor et al., 2009). Over 80% of Philippine reefs are threatened by overfishing (Burke et al., 2002) and management actions such as bans on destructive fishing practises are often not adequately enforced (Licuanan and Gomez, 2000). Establishment of marine reserves is an important tool for community-based coastal resource management in the Philippines (Alcala and Russ, 2006; Maliao et al., 2009b), and there are currently over a thousand marine reserves implemented in the country (Arceo et al., 2008). However, over 80% of these marine protected areas are less than 1 km² in size (Arceo et al., 2008) and there has been no effort to address the efficacy of marine reserve design in a coordinated way at regional scales.

Threats associated with coastal development and land-use changes affect approximately 40% of reefs in the Philippines (Burke et al., 2002) and decreases in water quality associated with extensive aquaculture development are a major concern for reef health in several parts of the country (Primavera, 2006; Cruz-Trinidad et al., 2009). Empirical evidence indicates that the simultaneous effects of chronic local stressors such as sedimentation and nutrification reduces coral fitness, thermal tolerance and resilience to bleaching events (Carilli et al., 2009a, 2010; Wooldridge and Done, 2009). One event that is becoming more common is mass coral bleaching, in which corals expel their symbiotic zooxanthellae in response to thermal stress. Coral mortality resulting from such events is one of the most significant threats to reef health and function globally (Hoegh-Guldberg, 1999, 2004). Rapid increases in sea surface temperature (SST) have been a major factor in many large-scale coral bleaching occurrences in recent decades (Berkelmans et al., 2004; Lough et al., 2006) and increases in SST associated with climate change are predicted to result in higher frequency and severity of future mass coral bleaching events (Hoegh-Guldberg et al., 2007). Peñaflor et al. (2009) report a higher rate of SST increase around the Philippines over the period 1985-2006, as compared to other areas in the Indo-Pacific.

Given evidence that low water quality and coral bleaching can act synergistically to reduce coral cover, i.e. the combined impact of both stressors is greater than the sum of individual impacts (Carilli et al., 2009a, 2010; Wooldridge and Done, 2009), managing water quality is likely to be an important lever for increasing resilience to coral bleaching in coming decades. Modelling can be very helpful in (i) examining the probability of synergistic effects at local scales, (ii) identifying any emergent patterns of synergism at regional scales, and, in particular, (iii) exploring possible reef futures under alternative management responses at regional scales.

Aims

In this chapter we ask two questions regarding our model system:

- (i) Is the model portable, i.e. can a version of the model (which was developed initially for the Meso-American Reef system in the western Caribbean) applied to the Philippines region of the South China Sea realistically capture reef dynamics in the region?
- (ii) Assuming that the model adequately captures dynamics of South China Sea reefs, how can it be used to inform coral reef management decisions in the region?

We address the first of these aims by using complementary approaches to model validation. We first evaluate model behaviour under ‘healthy’ reef conditions, and then examine model trajectories under a series of perturbations. Importantly, patterns of regional-scale larval connectivity inform model behaviour and have implications for identifying appropriate spatial scales for management actions.

In addressing our second aim we investigate two sets of regional-scale scenarios that relate to current threats to coral reef health in the region. In the first set of scenarios we explore how the model can be used to assess the efficacy of marine reserve placement, an important issue sensitive to patterns of larval connectivity. The importance of considering local- to regional-scale larval connectivities in marine reserve design has been increasingly recognised (Jones et al., 2009; Steneck et al., 2009), particularly in the context of building resilience to climate change impacts (McLeod and Leslie, 2009). We assess the effectiveness of different schemes for marine reserve placement by comparing modelled recovery trajectories for fish stocks and coral cover. In the second set of scenarios we examine the regional-scale implications of increased frequency of coral bleaching events and ask how differences in water quality might affect the resilience of reef systems to coral bleaching in the future. These scenarios demonstrate how CORSET can be used as a tool to evaluate environmental outcomes of alternative management actions and to identify particular localities for which management actions are likely to be most effective.

4.2 Model components

Ecological dynamics

The components of CORSET are: (i) a gridded base-map of the region of interest, identifying the location of coral reef cells (Figure 4.1B); (ii) independent instantiations of a local-scale mean-field model of ecological dynamics (Fung, 2009) in each coral reef grid cell; and (iii) larval connectivity matrices detailing transition probabilities between larval sources and sinks. Fung’s (2009) local model captures key dynamic processes for shallow coral reef systems ($\sim 5 - 20$ m depth), for example coral-macroalgal ‘phase-shift’ transitions (Knowlton, 1992; Mumby et al., 2007b), as well as distilling a set of interactions that are readily parameterised for reefs in different biogeographic regions. Here it is defined by difference equations (which were derived from Fung’s 2009 continuous-time equations using Euler’s method; see Appendix A) that describe interactions between nine coral reef functional groups: brooding corals, spawning corals, macro turf, macroalgae, grazed epilithic

algal communities (EAC), herbivorous fish, small-to-intermediate piscivorous fish, large piscivorous fish and sea urchins (Table 4.1). State variables in the local model are proportional covers of benthic groups (corals and algae), and biomasses of consumer groups (fish and sea urchins), and the local model pertains to spatial scales in the order of hundreds of metres to several kilometres. Because the model does not describe fine scale dynamics (i.e. at scales of 1 – 100 m), we do not model growth of corals or algae across cell boundaries, or the movement of fish between cells. We have considered only those fish that are reef-associated.

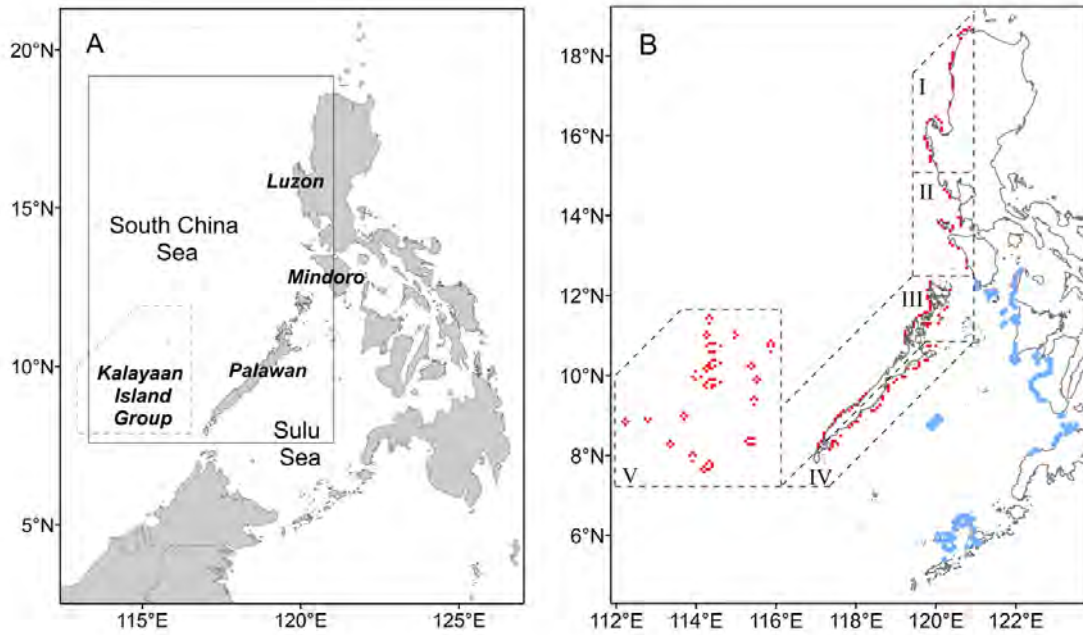


Figure 4.1: (A) Spatial extent of the region modelled for Philippines/South China Sea (PSCS) instantiation of CORSET. (B) The location of reef cells is indicated in red. Each $9 \text{ km} \times 9 \text{ km}$ block is divided into nine $3 \text{ km} \times 3 \text{ km}$ cells. Reef cell locations were extracted from reef distribution maps from Conservation International’s coral reef mapping project. Areas delineated by dashed lines in (B) indicate the extent of the five subregions; I (northern and central Luzon), II (southern Luzon and Mindoro), III (western Palawan), IV (eastern Palawan) and V (the Kalayaan Island Group). Offshore reefs in western Palawan (subregion III) are not included as these reefs are mostly mesophotic ($> 30 \text{ m}$ depth). Blue circles represent external larval source locations in the Sulu Sea.

The local-scale model is instantiated in each $3 \text{ km} \times 3 \text{ km}$ reef cell of a base-map for the Philippines/South China Sea region (here-on referred to as the PSCS region). The dimensions of the base-map grid are 388×489 cells, 2262 of which are classified as coral reef cells. Reef cells are connected by regional-scale dispersal and subsequent settlement of spawning coral, fish and sea urchin larvae. Settled larvae recruit to adult populations after one year. Post-settlement mortality modelled during this first year is described in Appendix B and includes density dependent effects

for fish and sea urchin recruits. The majority of model parameters for the PSCS instantiation of CORSET are defined as ranges (Table A1, Appendix A) and have been derived from a large body of literature as well as unpublished ecological data from the Philippines. Values are selected at random from these ranges (i.e. assuming a uniform distribution) for each reef cell in the model and are allowed to vary from year-to-year. The updating interval for CORSET is one week, with model output recorded every year. A weekly updating interval ensures mathematical rigour (small updating intervals reduce the number of mathematical constraints required to keep the model within the biological domain) and is realistic in terms of computational cost. CORSET is implemented in the open source object-oriented Python Programming Language (Python Software Foundation, Hampton, New Hampshire, USA) version 2.5.

Table 4.1: Definitions of functional groups modelled, with example taxa for the Indo-Pacific.

Functional group	Description
Brooding corals	Hermatypic coral species with internal brooding of planula larvae followed by release of planulae (e.g. <i>Acropora palifera</i> , <i>Pocillopora damicornis</i> , <i>Seriatopora hystrix</i>)
Spawning corals	Hermatypic coral species with broadcast spawning and external fertilization of gametes (e.g. most <i>Acropora</i> spp., <i>Montipora</i> spp.).
Macroturf	Fast growing, filamentous algae that form patches greater than $\sim 2 - 4$ mm canopy height (e.g. <i>Hersiphonia secunda</i> , <i>Polysiphonia scopulorum</i> , <i>Spyridia filamentosa</i>).
Macroalgae	Green, red and brown algae with larger thallus size and greater structural complexity than macroturf (e.g. <i>Sargassum</i> spp., <i>Lobophora variegata</i>).
Grazed epilithic algal community (EAC)	Benthic cover characterized by non-geniculate coralline algae, dead coral skeletons and cropped filamentous algae. For purposes of the model, the most important feature of this functional group is that it is covered by fine algal turf less than $\sim 2 - 4$ mm in height. The low canopy height of this fine turf is maintained by intensive grazing.
Herbivorous fish	Reef associated fish that feed on EAC, macroturf and macroalgae (e.g. families Acanthuridae, Scaridae, Siganidae).
Small-to-intermediate piscivorous fish	Fish that predate on herbivorous fish and are < 60 cm in length. Some fish in this functional group remain small-to-intermediate throughout their lifetime (e.g. some fish from families Lutjanidae, Serranidae), while a certain proportion grow into large piscivorous fish.
Large piscivorous fish	Fish that predate on herbivorous fish and small-to-intermediate piscivorous fish and are ≥ 60 cm in length (e.g. fish from families Carangidae, Lutjanidae, Serranidae).
Sea urchins	Grazing sea urchins (e.g. <i>Echinothrix</i> spp., <i>Diadema setosum</i>).

Dispersal simulations

Larval dispersal information for the PSCS region was derived from monthly particle tracking simulations (using the HYbrid Coordinate Ocean Model HYCOM) for release nodes around the coasts of Philippine, Malaysian and South China Sea islands within the domain 112°E-128°E, 4°N-22°N. HYCOM is a 3-dimensional circulation model that applies for both the open ocean and shallow coastal seas and includes wind-driven mixing (Bleck, 2002). Release nodes were 9 km × 9 km grid cells from which 100 buoyant particles were released at the beginning of each dispersal simulation. Simulations were conducted for ‘passive’ and ‘active’ particles; active particles were able to sense and swim towards suitable settlement habitat after a specified pre-competent period. We processed dispersal simulation outputs for passive and active particles to obtain connectivity matrices, which describe transition probabilities from source to sink locations for spawning corals, fish and sea urchins. Processing involved: (i) filtering release nodes by correspondence with actual reef locations in the PSCS region (this was necessary since dispersal simulations were conducted for contiguous release nodes along coastlines in the model domain, and so a proportion did not coincide with coral reef locations); (ii) extracting dispersal patterns for appropriate reproductive seasons for each functional group (i.e. corals, fish and sea urchins); and (iii) applying larval mortality.

Filtering the dispersal simulation output yielded 249 release nodes corresponding with the location of coral reefs (where reef locations were derived from Conservation International’s coral reef mapping project), reduced from an initial 2198 coastal nodes. The resultant grid is the same as the base-map for the PSCS instantiation of CORSET but at a coarser resolution of 9 km × 9 km. From dispersal simulations for the entire Philippine-Malaysian-SCS domain described above we identified source nodes outside the PSCS region that are likely to act as important larval sources for reefs within our model region. Accordingly, we included an additional 126 ‘external’ source nodes in the Sulu Sea (Figure 4.1B). These are represented as sources in connectivity matrices for corals, fish and sea urchins, but do not act as sinks. Ecological dynamics are not modelled for external source nodes, but the assumed cover/biomass at these locations is taken as the average of cells in the model domain at each time step. With the exception of the Sulu Sea, it is unlikely that other reef areas outside the PSCS region (but within the larger dispersal simulation domain) are important sources of larvae to reefs within the region.

Biological parameters used to derive larval connectivity from dispersal simulation data are presented in Table 4.2. For fishes, we assumed that competent larvae actively swim towards reefs within a distance of 9 km (as in Paris et al., 2007), while coral and sea urchin larvae behave as passive particles. We took the average of monthly transition probabilities from dispersal simulations (over the reproductive seasons specified in Table 4.2) to obtain connectivity matrices for the three functional groups. Larval mortality was assumed to be exponential and was applied as: *arriving larvae* = *raw larvae* × $e^{-m \times d}$, where m and d are the daily mortality rate and larval dispersal period in days, respectively (from Morgan, 1995).

Table 4.2: Biological parameters used to generate connectivity matrices.

	Coral larvae (spawning species)	Fish larvae	Urchin larvae
Dispersal mode	passive	active	passive
Spawning season	March – May ^(a,b)	year round	year round
Dispersal period (days) ^(c)	30 ^(d,e)	40 ^(f)	40
Mortality (day ⁻¹)	0.2	0.1 ^(f)	0.2

^(a)Bermas et al. (1993), ^(b)Vicentuan et al. (2008), ^(c)all larvae are assumed to be pre-competent (unable to settle) for 5 days following spawning, ^(d)Baums et al. (2006), ^(e)Richmond and Hunter (1990), ^(f)Paris et al. (2007).

4.3 Regional-scale larval connectivity

Despite differences in larval behaviour and mortality rates, broad patterns of simulated connectivity were similar for fish, coral and sea urchin functional groups, although the settlement signal was sparser for corals (Figure 4.2) as a result of their limited seasonal dispersal period (March – May rather than year round; Table 4.2). Four distinctive patterns of larval connectivity within and between PSCS subregions emerged (Figure 4.2A, B and C):

- (i) diffuse self-recruitment at a subregional scale (e.g. subregion V);
- (ii) strong self-recruitment to natal reefs, i.e. at the scale of 9 km × 9 km reef cells (e.g. subregion IV);
- (iii) supply of larvae from a small set of source reefs to a diffuse set of settlement reefs (e.g. from subregion III to subregion V); and
- (iv) supply of larvae from a broad set of source reefs to a narrow set of settlement reefs (e.g. from subregion V to subregion III).

Reefs in the Sulu Sea act as larval sources for reefs in all subregions, but the simulated settlement signal is much stronger for reefs in subregion IV (Figure 4.2D). This is unsurprising given that eastern Palawan (subregion IV) forms the western border to the Sulu Sea (Figure 4.2). However, some larvae clearly escape at the northern and southern ends of the Palawan land mass to supply reefs in other subregions. As for subregional-level connectivity, simulated larval supply from Sulu Sea reefs for corals and sea urchins followed a similar pattern to that identified here for larval fish. Larval exchange between the Kalayaan Island Group (subregion V) and western Palawan (subregion III) is evident for all three groups. Understanding patterns of larval connectivity aids interpretation of the behaviour of our model under healthy and perturbed conditions. This behaviour is examined in the following section.

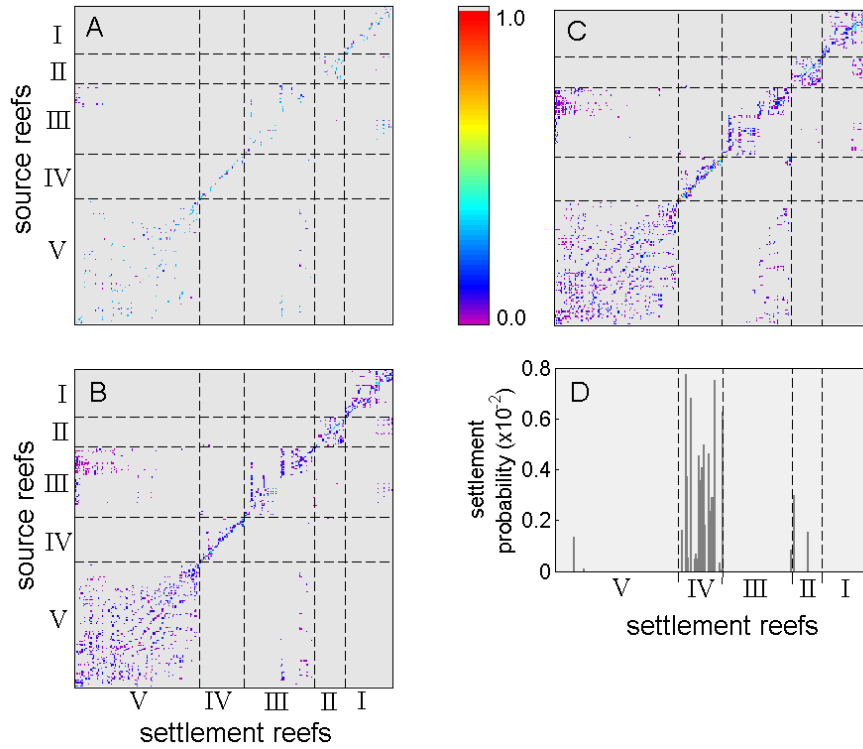


Figure 4.2: Matrices of transition probabilities between source reefs and settlement reefs for coral (A), sea urchin (B) and fish (C) larvae in the PSCS region. Matrices are derived from the results of particle tracking simulations (using the HYbrid Coordinate Ocean Model HYCOM). The matrix for coral larvae applies for spawning corals only; brooded coral larvae settle locally. Values are standardized relative to the maximum recruitment probability for each group. Dashed lines indicate spatial delineations for source and settlement reefs in the five subregions (I – V). Self-recruitment is represented along the upward diagonal axis. Settlement probabilities for fish larvae originating in the Sulu Sea (D) indicate a strong settlement signal in subregion IV (eastern Palawan).

4.4 Model validation

We validated the PSCS instantiation of CORSET by asking two questions:

- (i) Can the model reproduce community structure typical of a ‘healthy’ Philippines reef in the absence of any external forcings?
- (ii) Does the model reproduce broad-scale dynamics for the PSCS region over the past 50 years given a schedule of known forcings?

Here we use the term ‘forcings’ to refer to disturbances and stressors in the form of fishing pressure, destructive fishing activity, damaging storms, coral bleaching, disease, crown-of-thorns starfish (COTS) outbreaks, nutrification (*sensu* Szmant, 2002) and sedimentation. These forcings are modelled as losses of cover/biomass or as parameter scalings (Table 4.3). Effects and magnitudes of forcings are parameterised from the literature.

Table 4.3: Implementation of forcings in CORSET.

Forcing	Implementation
Fishing pressure	Fishing pressure is modelled as a decrease in fish biomass that is apportioned between herbivorous, small-to-intermediate piscivorous and large piscivorous fish groups (see Appendix A). Fishing pressure can change over time and appropriate values are derived from the literature depending on the scenario of interest.
Destructive fishing	Decreases coral cover by $0.4 - 3.2\% \text{ yr}^{-1}$ ^(a) . This includes adverse effects of dynamite fishing, cyanide fishing and <i>muro-ami</i> ^(b) on coral cover.
Typhoons	Typhoons ^(c) are modelled as a decrease in coral cover by a factor of $0.002 - 0.7$ ^(d,e,f,g,h) , and a decrease in macroalgal cover by a factor of 0.9 ⁽ⁱ⁾ . High category typhoons affect a greater proportion of reef cells than low category typhoons ^(f) . Category 4 and 5 typhoons are assumed to affect all cells within a reef tract (or subregion), category 3 typhoons affect two thirds of cells, and category 1 and 2 typhoons affect one third of reef cells.
Coral mortality events	Coral bleaching, disease and crown-of-thorns outbreaks decrease coral cover. The severity of individual events is derived from the literature.
Nutrification	Increases macroalgal growth by a factor of $2 - 7$ ^(j,k,l,m,n) and decreases coral larval production by a factor of $0 - 0.25$ ^(o,p) .
Sedimentation	Increases coral mortality by $0 - 0.2 \text{ yr}^{-1}$ ^(q) , decreases survival of coral recruits by a factor of 0.6 ^(r) and prevents recruitment of coral onto macro turf ^(s) .

^(a)McManus et al. (1997), ^(b)*Muro-ami* is a destructive fishing technique which uses a drive-in-net and weights on vertical scare lines (McManus, 1996; Miclat et al., 1991), ^(c)Typhoons are tropical cyclones with maximum sustained wind speeds $\geq 33 \text{ m/s}$ (Nyberg et al., 2007), ^(d)Bythell et al. (1993), ^(e)Cheal et al. (2002), ^(f)Gardner et al. (2005), ^(g)Lirman (2003), ^(h)Wantiez et al. (2006), ⁽ⁱ⁾Mumby et al. (2006), ^(j)Lapointe (1989), ^(k)Lapointe and O’Connell (1989), ^(l)Larned and Stimson (1996), ^(m)Larned (1998), ⁽ⁿ⁾Schaffelke and Klumpp (1998), ^(o)Loya et al. (2004), ^(p)Ward and Harrison (2000), ^(q)Nugues and Roberts (2003), ^(r)Babcock and Smith (2000), ^(s)Birrell et al. (2005).

To address validation question (i) we ran the model over a long time series (100 years) without any forcings and compared average values of state variables with expected values of community composition on healthy Philippine reefs. Expected values for a healthy reef were derived from (a) empirical observations from reefs in the Philippines with particularly high coral cover and/or fish biomass (Russ et al., 2005; PhilReefs, 2005, 2008; MERF/MSI, 2008) and (b) indicator values for ‘good’ to ‘excellent’ coral cover and ‘high’ to ‘very high’ fish biomass (Nañola et al., 2006). Results of this approach showed that modelled values of benthic cover for coral, grazed EAC and algae were within expected ranges for a healthy reef (Figure 4.3A) as were piscivorous fish biomasses (Figure 4.3B). Simulated herbivorous fish biomasses were slightly higher than expected on some reefs in subregions II and V. Published estimates for sea urchin biomass on healthy Philippine reefs are not available, however observed urchin biomasses for reefs in Bolinao (Pangasinan province, Luzon) are between 0 – 7 g/m² (R. Geronimo, unpublished data). Our modelled values for sea urchin biomass fell within this range in all subregions.

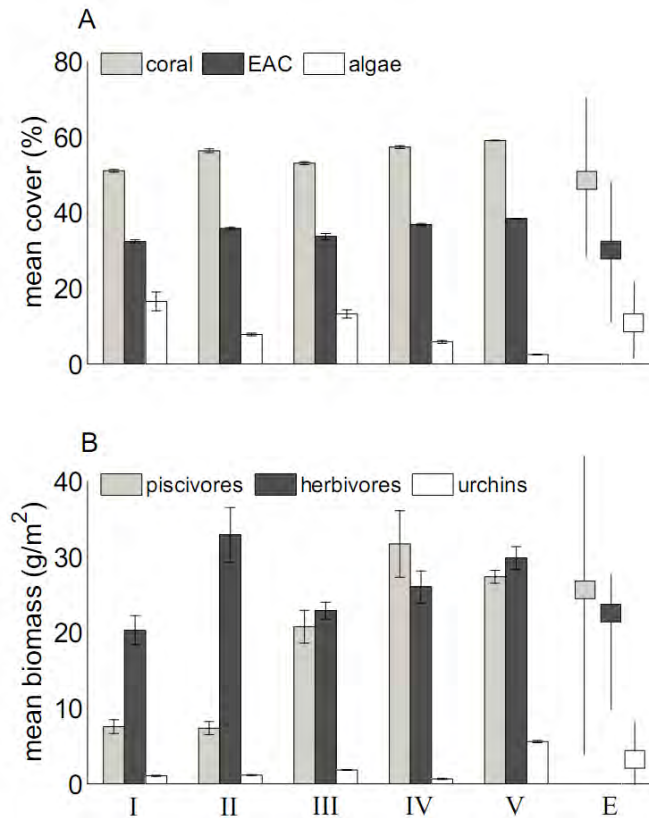


Figure 4.3: Average endpoints \pm 95% confidence intervals for (A) benthic and (B) consumer functional groups from five 100-year model runs in the absence of forcings (the ‘healthy reef’ scenario). Endpoints represent equilibrium values for the five subregions (I – V) and error bars indicate variability between model runs. Values for algae in (A) are the sum of macoralgal and macro turf covers, and biomass values for piscivores in (B) are the sum of model outputs for small-to-intermediate and large piscivorous fish. Vertical bars and shaded boxes to the right (E) indicate expected ranges and mean values, respectively, for healthy reefs in the PSCS region (derived from empirical observations and indicator values).

Average modelled coral and algal cover was generally consistent between subregions. This is in contrast to fish functional groups, for which the ratio of herbivorous to piscivorous fish biomass was spatially variable. This variability is related to differences in self-recruitment and external larval supply. Total modelled fish biomass was highest in subregion IV and lowest in subregion I. This is consistent with fish larvae being entrained within the Sulu Sea and hence supplying eastern Palawan, and relatively lower settlement of fish larvae in northern Luzon where the dominant ocean currents are stronger and more directional towards the north (Morton and Blackmore, 2001). Model trajectories under the ‘healthy reef’ scenario were stable over the simulation period of 100 years.

We assembled an historical timeline of disturbance events and anthropogenic stressors which have affected PSCS reefs over the period from 1960-present to address validation question (ii) (Figure 4.4). We did not include the 1991 Mt. Pinatubo eruption in our timeline because of limited information regarding the spatial extent and the nature of effects of ash fall on Philippine coral reefs (Ochavillo et al., 1992). We inferred changes in fishing pressure for each subregion over time, assuming nominal fishing activity in 1960, a linear increase to maximum fishing pressure in the 1980s, and a slight decrease in fishing pressure from 1990-present (for subregions I – IV only). We based the magnitude of fishing pressure on recent published estimates for the Philippines (Licuanan and Gomez, 2000; Alcala and Russ, 2006). Estimates for fishing pressure in the Philippines do not apportion reported catches between trophic groups. Nonetheless, we assumed higher fishing pressure for herbivorous fish than for piscivorous fish, reflecting that stocks of piscivorous species are markedly depleted on the majority of Philippines reefs (PhilReefs, 2005). We did not include potential effects of marine reserves on spatial variability in fishing pressure because of uncertainty about the level of enforcement of various reserves, and because the spatial scale of the majority of marine reserves in the Philippines ($< 1 \text{ km}^2$; Arceo et al., 2008) is much smaller than the scale of our base-map grid. The proportion of reef cells affected by nutrification and sedimentation in subregions I and II was assumed to have increased linearly over time from nominal impacts in 1960 to values derived from Burke et al.’s (2002) Reefs at Risk analysis (namely the proportion of reefs in these subregions at ‘very high’ risk from coastal development, a proxy for nutrification, and sedimentation). Threat estimates from Burke et al. (2002) were used in the same manner to assign destructive fishing impacts. We assumed a peak in destructive fishing activity between 1980-1990 in all subregions.

Agreement between model trajectories for 1960-present and available empirical data was satisfactory (Figure 4.5; see Table C2, Appendix C for a summary of validation data sources). There was a tendency for the model to under-estimate coral recovery following the 1998 bleaching event in subregions I, II and IV. This may be because published estimates of bleaching-induced coral mortality (Arceo et al., 2001), determined from surveys of a limited number of sites but applied broadly in our historical forcing schedule, were too high. Modelled values for coral cover in the Kalayaan Island Group (subregion V) were generally higher than reported values, although observations of coral cover in this subregion are limited ($n=1$ in 1993 and 1996, and $n=3$ in 1999). There was a high degree of spatial variability in modelled algal cover, reflecting local depletion of grazer biomass in some reef cells. Observations of fish biomass refer to total fish biomass (including fish species in functional groups not represented here), hence we would expect model predictions of fish biomass (the sum of herbivorous and piscivorous fish functional groups only) to be lower than observations, as is generally the case in subregions I, II and III. Model predictions of fish biomass in subregion IV may be too high, although we note again that observations for this subregion

during the validation period are limited (n=5 in 2001, 2004 and 2007). Given the results from our two approaches to model validation we can be confident in using the model to address questions relevant to coral reef management at a regional scale. We do this using scenario testing to envisage possible reef futures under alternative management strategies.

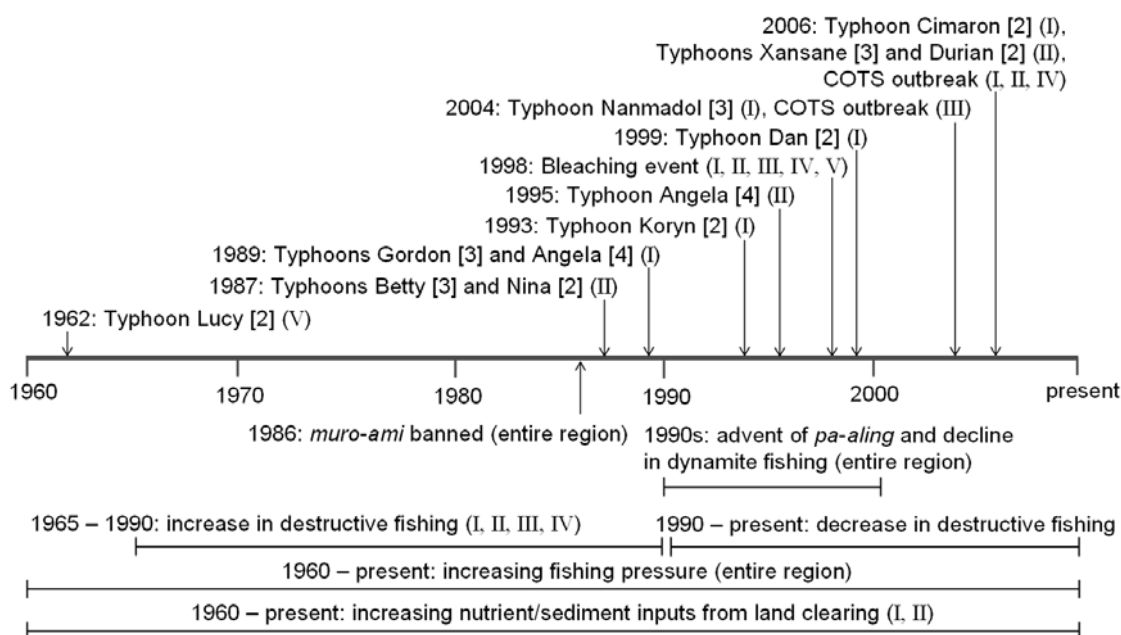


Figure 4.4: Historical timeline for the PSCS region from 1960-present. Numbers in square brackets following typhoon names refer to typhoon strengths at the time they intersected reef areas (JTWC, 2009) and roman numerals in parentheses following each event refer to the PSCS subregions affected (Figure 4.1B). COTS refers to the corallivorous crown-of-thorns starfish (*Acanthaster planci*). *Muro-ami* is a destructive fishing technique that uses weights on vertical scare lines to herd reef-associated fish towards nets (McManus, 1996; Miclat et al., 1991). This technique has been mostly replaced by *pa-aling* which uses bubbles generated by surface-supplied compressed air pumped through plastic hoses, rather than weighted lines, and is hence less damaging to coral cover (Miclat et al., 1991).

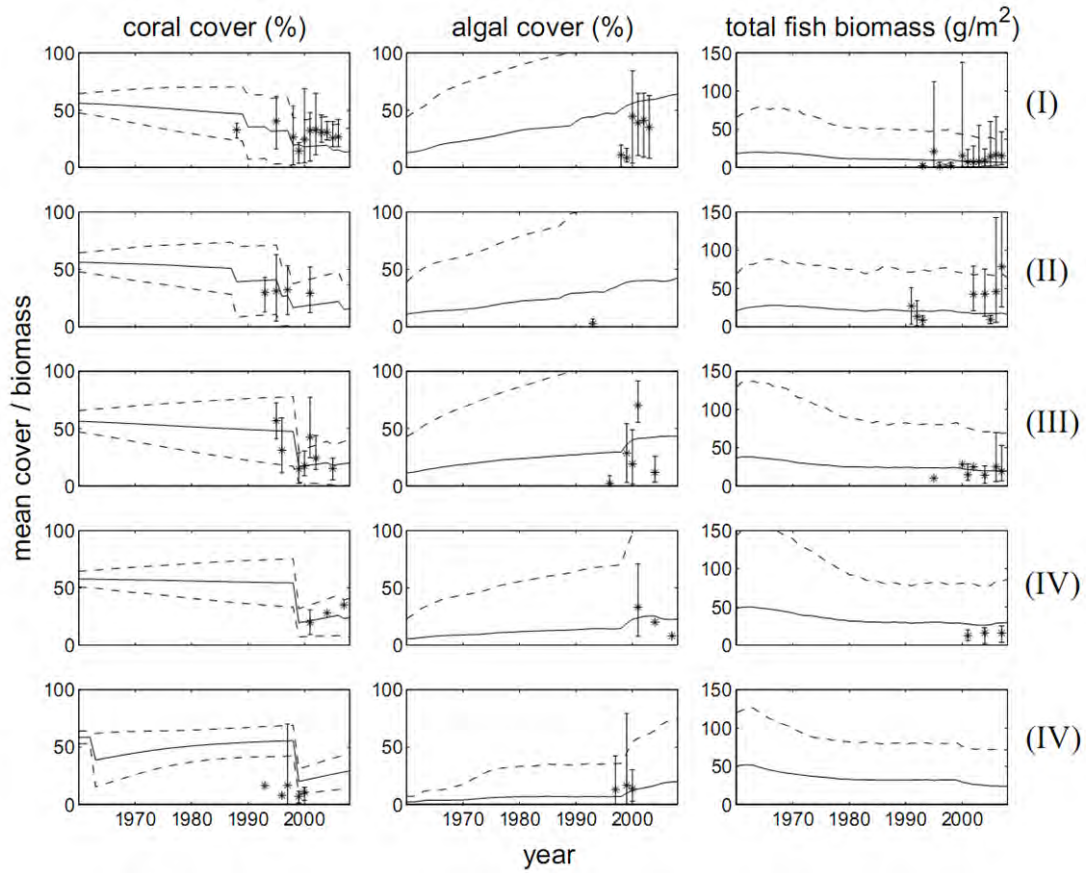


Figure 4.5: Comparison of model trajectories (including known forcings) for coral cover, algal cover and total fish biomass in the five PSCS subregions (I – V) from 1960-present with empirical observations. Solid lines indicate mean trajectories from five model runs, and dashed lines indicate 95% confidence intervals across all reef cells within each subregion. Vertical bars and stars indicate minimum-maximum ranges and average values from observations, respectively (see Appendix C for validation data sources). Algal cover refers to macroalgal and macro turf covers combined, and total fish biomass is the sum of herbivorous and piscivorous fish biomasses.

4.5 Scenario testing

Marine reserves

To assess the effects of marine reserve placement on recovery of fish biomass and coral cover in the PSCS region we examine two heuristic scenarios:

- (i) reefs that act as important larval sources for fish at a *regional scale* (i.e. where connectivity between reef cells is considered across subregions) are assigned as no-take marine reserves; and
- (ii) reefs that act as important larval sources for fish at a *subregional scale* (i.e. where connectivity between reef cells is considered within subregions) are assigned as no-take marine reserves.

Under both scenarios 10% of total reef area in the PSCS region was designated as no-take marine reserve. In scenario (i) we calculated cumulative settlement probabilities (i.e. total larval supply across all sink locations) for fish larvae from each reef cell, and selected those cells with the highest cumulative probabilities. In the second scenario we calculated cumulative larval supply from all source reefs to reefs within each subregion. Thus, under this scenario one fifth of the total area designated as no-take marine reserve was allocated to the most important larval sources for each subregion. The area of individual marine protected areas in these scenarios ranged between 3 km \times 3 km – 9 km \times 9 km. We assumed zero fishing in protected areas (i.e. effective compliance) and examined regional-scale trajectories for fish stocks over a 50-year period.

Recovery of herbivorous fish biomass and coral cover was better under scenario (ii) than under scenario (i), but under both scenarios was limited for piscivorous fish (Figure 4.6). Fish biomass and coral cover remained low in subregions I and II under scenario (i) relative to scenario (ii). This is because the regional-scale method of reserve allocation did not protect a sufficient number of reefs in subregions I and II from fishing pressure, and did not protect reefs that act as key larval sources for subregions I and II, resulting in limited replenishment of fish biomass and grazing pressure. This highlights the importance of considering subregional-scale processes in using larval connectivity information to design marine reserves.

A temporal lag in response to marine reserve implementation is particularly evident in trajectories for algal cover (Figure 4.6D). This lag most likely reflects that grazer biomass needs to recover to some critical level before any reduction in algal cover is achieved. Herbivorous fish biomass and coral cover were predicted to be highest on reefs in the Kalayaan Island Group irrespective of reserve design. There may be longer-term regional-scale benefits for reef health from maintaining well managed reefs in this area, particularly given vulnerabilities to climate change impacts which are addressed in the following section. Limited recovery of piscivorous fish populations in subregions I and II under either scenario highlights that other management approaches for limiting catches (outside no-take reserves) are likely to be needed to facilitate recovery of these fish stocks.

In light of this we examined a further scenario – ‘combined management’ (Figure 4.6C and F) – which combines marine reserve design from scenario (ii) with a 20% reduction in fishing pressure in subregions I and II, and a decrease in the accessibility of fish to fishermen across the entire PSCS region. A decrease in accessibility was achieved by altering the fishing accessibility parameter

in the local model (see Appendix A) by an order of magnitude. This is equivalent to reducing fishing efficiency by approximately 5-10% (within the range of fish biomasses modelled). Under this scenario there was a 90% increase in the recovery of piscivorous fish biomass after 50 years across the five subregions compared with scenario (i) and a 65% increase compared with scenario (ii). In a management context this benefit would need to be balanced against the cost of reduced catches under lower fishing effort and efficiency.

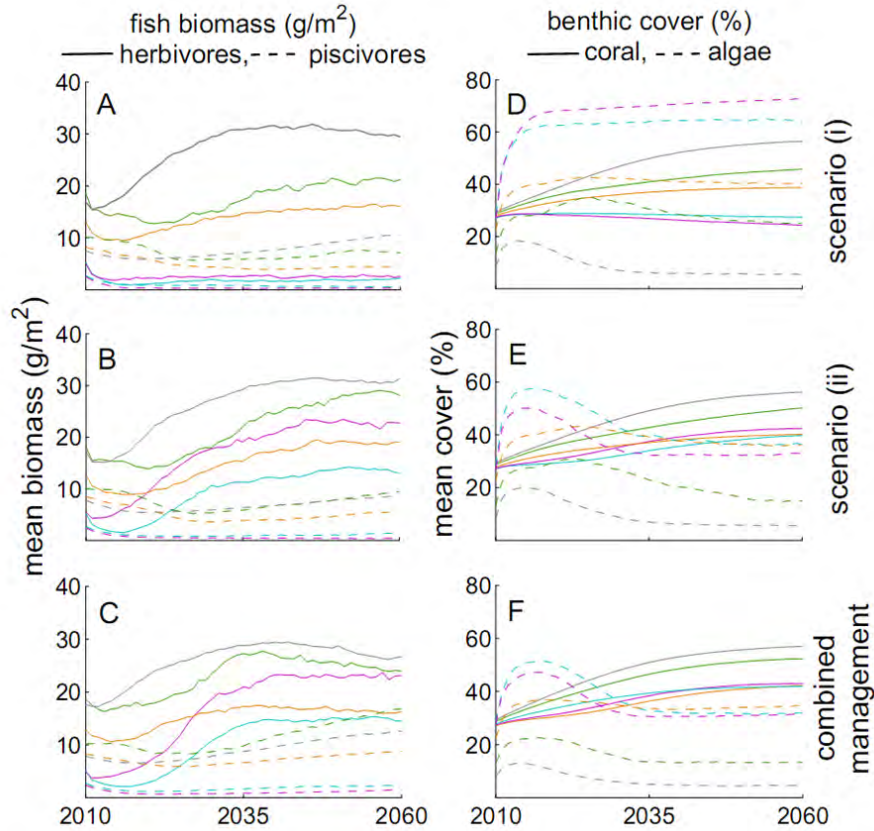


Figure 4.6: Model trajectories from five model runs for mean fish biomass (A, B and C) and benthic cover (D, E and F) in the five PSCS subregions (subregion I = blue, II = purple, III = orange, IV = green and V = grey). Results are presented for a 50-year simulation period under two scenarios for marine reserve placement (A, B, D and E), and one scenario of combined management approaches (C and F). In scenario (i) 10% of reefs that act as important larval sources for fish at a *regional* scale were allocated as no-take marine reserves, while in scenario (ii) reefs that act as important larval sources for fish at a *subregional* scale were selected as marine reserves. There was better overall recovery of coral cover and fish stocks under scenario (i) than under scenario (ii), although piscivorous fish biomass remained low in some subregions. The combined management scenario, in which fishing pressure in subregions I and II was reduced, and fish were less accessible to fishermen, was most successful in terms of recovery of piscivorous fish stocks.

Coral bleaching and water quality

We used CORSET to examine (a) regional-scale consequences of increased frequency of coral mortality associated with mass bleaching events in the PSCS region, and (b) potential interactions between increased coral bleaching frequency and low water quality (modelled as nutrification and sedimentation effects; see Table 4.3). We explored scenarios in which bleaching-associated mortality occurred with a long-term average frequency of once per decade and twice per decade (Donner et al., 2005; Donner, 2009), with random year-to-year occurrence. We note that some predictions for bleaching frequency in the twenty first century are more severe than those used here; Hoegh-Guldberg (1999) predicts biennial or annual events for a majority of the world's reefs by 2100. Our scenarios consider only events that are likely to cause mortality on the scale of the 1998 bleaching event in the Philippines (Arceo et al., 2001). Spatial distributions of thermal stress for the period 1985-1995 (Peñaflor et al., 2009) were used to infer reef locations in the PSCS region that are likely to suffer bleaching-induced mortality in coming decades. Peñaflor et al. (2009) found that reef locations in the northernmost Philippines, together with areas in northern Palawan and the Kalayaan Island Group, were subject to the highest bleaching-level stress during years of strong positive SST anomalies.

Results from five scenarios (2010-2060) are presented:

- (i) 20% of reefs in subregions I – IV are affected by nutrification and sedimentation (NS) – no coral bleaching
- (ii) Coral bleaching events (and associated mortality) occur with a long-term frequency of once every 10 years (BL10)
- (iii) Bleaching events occur with a long-term frequency of once every 5 years (BL5)
- (iv) Scenario (ii) with 20% of reefs in subregions I – IV affected by nutrification and sedimentation (BL10+NS)
- (v) Scenario (iii) with 20% of reefs in subregions I – IV affected by nutrification and sedimentation (BL5+NS)

Average coral and algal cover in 2060 under these five scenarios is compared with that on simulated healthy reefs not subject to any stressors (scenario H). There is evidence of a significant interaction between the effects of bleaching, nutrification and sedimentation for the PSCS region under scenarios BL10+NS and BL5+NS, with a disproportionately greater decline in coral cover than would be expected from the sum of impacts of the individual forcings of bleaching and reduced water quality (Figure 4.7). The simulated decline in coral cover under BL10+NS was 13% greater than expected from the sum of declines under BL10 and NS, and similarly for BL5+NS the decline in coral cover under combined forcings was 9% greater than expected from the sum of individual forcings. Interaction effects formally identify synergies which in this case arise because the effect of the combined stressors exceeds the sum of effects of individual stressors (Dunne, 2010). Nutrification, sedimentation and coral bleaching all significantly increased algal cover, but there was no evidence of synergistic effects in this case.

High frequency bleaching combined with nutrification and sedimentation (BL5+NS) was the only scenario under which we found evidence of a potential phase shift from a coral-dominated to an algal-dominated state. Somewhat surprisingly, algal cover was not dominant after 50 years under decadal bleaching combined with nutrification and sedimentation impacts (BL10+NS), suggesting that coral cover was able to recover sufficiently between bleaching episodes despite chronic stress. However, additional forcings, in particular fishing activity, are likely to increase the probability of phase-shifts under coral bleaching scenarios. Under all scenarios coral cover was lowest in the Kalayaan Island Group (subregion V), reflecting that this area is particularly vulnerable to bleaching-level thermal stress (Peñaflo et al., 2009).

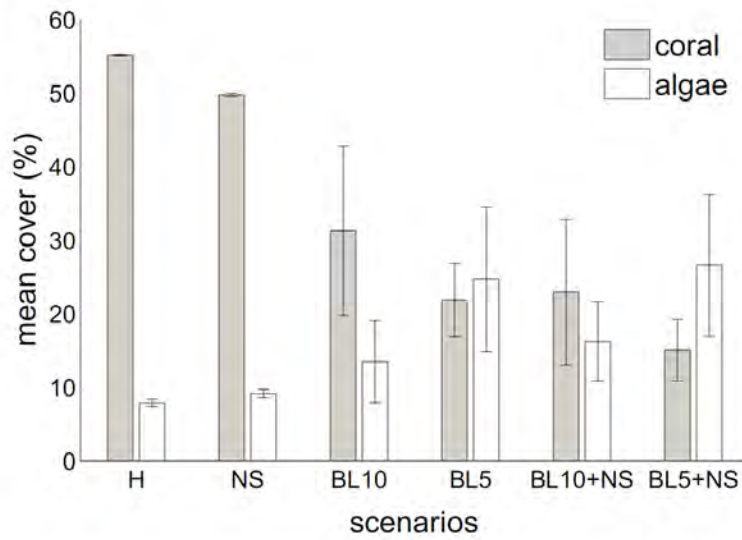


Figure 4.7: Comparison between average modelled values for benthic cover on healthy reefs (H) and benthic cover on nutrification/sedimentation affected reefs (NS) and under coral bleaching scenarios (BL). Values presented are mean coral and algal covers in 2060 under scenarios in which coral bleaching occurs with a long-term frequency of once per decade (BL10) and twice per decade (BL5). Error bars are 95% confidence intervals from 10 model runs. Algal cover refers to the sum of macroalgal and macro turf covers. Bleaching, nutrification and sedimentation act synergistically to reduce coral cover in scenarios BL10+NS and BL5+NS ($F_{2,54}=5.48$, $P=0.0068$ for interaction between NS and BL; log transformed coral cover data). Nutrification, sedimentation and bleaching significantly increased algal cover ($F_{1,54}=10.63$, $P=0.0019$ for NS and $F_{2,54}=211.52$, $P<0.0001$ for BL; log transformed algal cover data), but there was no evidence of a synergistic interaction in this case.

4.6 Discussion

Effective management of marine systems is challenging and complex, and requires novel, multi-disciplinary approaches (Hughes et al., 2005; Mumby and Steneck, 2008; Bradbury and Seymour, 2009). Coral reefs, and their associated ecosystem services, are at particular risk of severe degradation from a raft chronic anthropogenic stressors and from the projected impacts of climate change (Hoegh-Guldberg et al., 2007; Mumby and Steneck, 2008; Veron et al., 2009). Resource managers require tools that can capture the multi-level complexity of both biophysical processes and human activities that affect coral reef systems, but at the same time are accessible and simple to use and interpret. We have shown that our multi-scale model captures the characteristic dynamics of coral reef systems and can be applied in decision support contexts to evaluate potential reef futures under alternative management scenarios.

Model validation and the importance of considering larval connectivity

Model validation is an important step in any model building process (Nguyen and de Kok, 2007; Nguyen et al., 2007), particularly for models of complex systems such as coral reefs. Validation of the PSCS instantiation of CORSET demonstrates that the model is able to capture general patterns of change in reef community composition since 1990. Moreover, it identifies inherent differences in modelled reef state between subregions that are likely to have important consequences for reef functioning and resilience in particular localities. These differences are related to patterns of larval connectivity derived from dispersal simulations. Examining source-sink relationships through the use of larval dispersal simulations can provide important information for coral reef management at subregional and regional scales. For example, the Kalayaan Island Group (subregion V) has historically been poorly managed, in part due to political contention over sovereignty. Reefs in this subregion are important larval sources for western Palawan (subregion III), where self-recruitment is relatively low (Figure 4.2). Degradation of reefs in the Kalayaan subregion is likely to have flow-on effects for reef health (in terms of coral cover and fish biomass) in western Palawan. In this case, reef degradation would be compounded given that self-recruitment is high in the Kalayaan Island Group. If this reflects reality (and it may not if reefs outside the simulation area act as important larval sources for subregion V) then reefs in subregion V cannot be ‘rescued’ by larval input from elsewhere and are unlikely to recover unless causes of degradation are addressed.

CORSET demonstrates that regional- and subregional-scale biophysical connectivities are likely to play a significant role in determining reef health and recovery trajectories. While there are some examples of national-level actions to improve the management of coral reef resources in the Philippines (e.g. the national ban on *muro-ami* fishing in 1986), present governance structures focussed on local-scale decision making are arguably an impediment to cohesive regional-scale management. Functional overlaps and interests of national agencies often result in blurred responsibilities (White and Courtney, 2004) and examples of successful reef management are generally limited to highly local scales (DENR et al., 2001) in which coral reef management is the mandate of Local Government Units (LGUs). The results of our scenario testing urge that effective regional-scale management strategies (which complement local-scale efforts) are essential.

Scenario testing and decision support

We provide two examples of scenario testing that demonstrate how CORSET can be used to inform management responses to threats to reef health in the PSCS region. In our first example we used patterns of larval connectivity to inform marine reserve placement. Our results highlight that, while marine reserves can contribute to effective fisheries management (and undeniably provide a range of other benefits such as biodiversity reservoirs and scientific baselines) alternative, complementary management approaches outside reserves are important to achieve sustainable harvesting of coral reef (and many other) fisheries (Allison et al., 1998; Lubchenco et al., 2003).

The marine reserve scenarios we present are heuristic and ignore several important biophysical and socioeconomic processes that may influence reserve effectiveness. CORSET does not capture potentially beneficial spill-over effects of adult fish biomass from reserve to non-reserve areas (Russ et al., 2003; Abesamis et al., 2006a,b), as we do not model fish movement. It also neglects the potential role of nursery habitats such as mangroves and seagrass in maintaining fish stocks inside and outside marine reserves (Mumby et al., 2004; Mumby, 2006a). Perhaps most critically, we have not explicitly included different levels of enforcement of marine reserves and our scenarios assume compliance with no-take reserves. Maliao et al. (2009a) found a strong effect of level of enforcement in their meta-analysis of changes in coral reef fish populations in Philippine marine reserves. CORSET could be used to explore scenarios of varying levels of compliance, and hence to guide investment decisions relating to spatial or temporal allocation of enforcement effort.

In our second example we demonstrated that the modelled effects of low water quality can reduce reef resilience to coral bleaching events at a regional scale. In reality, issues of coral bleaching risk and water quality management are also likely to inform marine reserve design. Managers will be increasingly faced with decisions over whether to protect sites that are more or less prone to bleaching events or that may already be degraded because of chronic sedimentation and nutrification. While it is difficult to disentangle the threats in reality, simulation models such as CORSET provide a means to assess the effects of individual and combined stressors and disturbances and to evaluate different options for management in the light of combined effects. Moreover, information from models can be used in ‘management triage’ to help optimise cost effectiveness.

There are clearly many other factors beyond those in our examples here that will influence reef futures and decision making in relation to marine reserve design, water quality and coral bleaching risk in the Philippines and elsewhere. Other factors to be considered in designating marine reserves include compliance (as discussed above), extending existing reserves, the distribution of biodiversity, habitat heterogeneity and the presence of threatened species or vulnerable life stages (Roberts, 2003). In considering reef futures under climate change scenarios, potential effects of ocean acidification on reef accretion and stability are important (Hoegh-Guldberg et al., 2007). No single tool is appropriate to address the complexity of issues, and we advocate the use of CORSET in combination with other tools for natural resource management planning such as zoning protocols (e.g. Watts et al., 2009), fisheries assessment models (see Lachica-Aliño et al., 2006), and coupled social-ecological approaches (e.g. Cinner et al., 2009). Simulation models like CORSET can be usefully applied to identify a subset of management options for regional-scale environmental investment that are then evaluated subject to economic constraints (Marinoni et al., 2009).

Two important socioeconomic activities that influence reef health in the Philippines but which have not been addressed here are aquaculture and tourism. These industries have grown considerably in the Philippines in the past decade (Cruz-Trinidad et al., 2009). Given the complicated nature of socioeconomic drivers, impacts on reef health are arguably best addressed in the context of a coupled socioeconomic-biophysical system (e.g. McClanahan, 1995; Gribble, 2003; Little et al., 2007; Shafer, 2007; Cinner et al., 2009). The forcings applied in our study to recreate an historical timeline for the PSCS region, and to project scenarios (i.e. physical damage, harvesting, nutrification and sedimentation) can be used as ‘pipes’ for information transfer between CORSET and an agent-based socioeconomic model. In other words, CORSET is readily configured in a combined biophysical-socioeconomic approach (as is demonstrated in Chapter 5).

Caveats and uncertainties

Identifying sources of uncertainty is an important consideration in designing and applying complex systems models (Ascough II et al., 2008) and model validation functions to identify both the strengths and weaknesses of a model to its intended users (Nguyen and de Kok, 2007; Nguyen et al., 2007). A key uncertainty in CORSET relates to larval connectivity patterns. Larval connectivity in marine populations is highly stochastic (Siegel et al., 2008) and dispersal simulations such as those used here arguably oversimplify connectivity processes. In particular, the dispersal model for the Philippines does not include vertical migration or stochastic mortality, but both processes have been shown to influence simulated connectivity patterns for marine larvae (Paris et al., 2007). Predictions of larval connectivity patterns from dispersal simulations should be interpreted with some caution unless they have been cross-validated using population genetic and larval tagging techniques (Jones et al., 2009). Researchers are increasingly aware of the need to integrate oceanographic and molecular approaches in the study of marine connectivity (Botsford et al., 2009), and significant advances have been made in the field of ‘seascape genetics’ (Galindo et al., 2006; Selkoe et al., 2008). CORSET is amenable to sensitivity analysis of connectivity patterns derived using different methods and under different assumptions about larval behaviour. We did not model connectivity for macroalgal propagules because of a lack of data regarding this process, however Elmhirst et al. (2009) show that macroalgal connectivity can play an important role in reef resilience and recovery trajectories. Furthermore, CORSET does not include seasonality in growth, reproduction or disturbance. However, because we use a weekly updating interval, CORSET can be used to explore the sensitivity of modelled reef communities to the inclusion or exclusion of seasonal processes (see Chapter 2).

In complex systems models such as CORSET there are various approaches to modelling and visualising ecological variability, and each will provide different (and complementary) information about the behaviour of the model system. The choice of method will depend on the question(s) being asked by the model user. For example, within any particular model run presented here, parameters were allowed to vary randomly in space and time within predefined ranges (i.e. assuming a uniform distribution). Variability in average behaviour between model runs under this scheme is relatively small, particularly in the absence of external forcings (see Figure 4.3). However spatial variability in any given run is large, and the degree of variability is dependent on the functional group (Figure 4.5). Spatio-temporal variability is an inherent property of real reef systems, which suggests that these systems are also inherently unpredictable at some scales. This raises questions

about the utility of model predictions for particular local sites under alternative management scenarios. Parameter variation methods in CORSET are flexible and the user can explore differing assumptions about the form of parameter distributions and the nature of parameter variability in space and time. To explore the full spectrum of model behaviours, parameters in CORSET can be held fixed for each model run, and a large number of Monte Carlo simulations will generate a probability distribution of possible model outputs (illustrated in Chapter 2).

Conclusions

We demonstrate a decision support tool, CORSET, that can be used to compare potential reef futures under alternative management scenarios. We use a generic framework, so that our tool is portable between different reef systems. Despite our simplifying assumptions, CORSET is able to realistically capture broad dynamics of systems as dissimilar as the PSCS region (this chapter) and the Meso-American Reef system (Chapter 1), and to reproduce changes in state variables that are of interest to coral reef managers and other stakeholders. We show how CORSET can be used to inform management approaches for key threats to reefs in the PSCS region, namely overfishing, water quality and coral bleaching. Directions for future model development include (i) creation of a user-friendly interface, (ii) model refinement through interaction with end-users, and (iii) coupling biophysical and socioeconomic dynamics to capture diverse indicators of reef state.

Chapter 5

Coupling biophysical and socioeconomic models for coral reef systems in Quintana Roo, Mexican Caribbean

Abstract

Transdisciplinary approaches that consider both socioeconomic and biophysical processes are central to understanding and managing rapid change in coral reef systems worldwide. To date there have been limited attempts to couple the two sets of processes in dynamic models for coral reefs, and these attempts are confined to reef systems in developed countries. We present an approach to coupling two existing models for coral reef systems in the Mexican state of Quintana Roo. The first is a biophysical model which uses dynamic equations to capture local-scale ecological processes on individual reefs. These reefs are connected at regional scales by the ocean transport of larval propagules. The second model used in the coupled system is an agent-based socioeconomic model which simulates changes in tourism, fisheries and urbanisation in the Quintana Roo region. Despite differences in the formulation of the two models, we were able to successfully integrate them through a process of modification, synchronisation and the definition of information flows and feedbacks. A preliminary evaluation of the coupled model system indicates that the model gives reasonable predictions for fisheries and ecological variables and can be used to examine scenarios for future social-ecological change in Quintana Roo. We provide recommendations for where efforts might usefully be focused in future attempts to integrate models of biophysical and socioeconomic processes, based on the limitations of our coupled system.

5.1 Introduction

The socioeconomic welfare of millions of people in coastal populations worldwide depends on ecosystem services provided by coral reefs (Moberg and Folke, 1999). However, reef ecosystem function, and hence the provision of ecosystem services, is at severe risk due to human activities (Hoegh-Guldberg et al., 2007; Mumby and Steneck, 2008). Management of these threats requires novel approaches to decision making (Mumby and Steneck, 2008; Sale, 2008; Bradbury and Seymour, 2009). While successful management must be based on sound ecological science, the utility of environmental management depends critically on human behaviour (Mascia et al., 2003). Hence there is a need for transdisciplinary efforts to develop decision support tools for coral reef management (Bradbury and Seymour, 2009). Coral reef research to date has tended to focus on either biophysical dynamics or, to a lesser extent, socioeconomic dynamics. Even when considered separately, biophysical and socioeconomic systems are complex and difficult to understand, and the interactions between the two are necessarily complex (Dizon and Yap, 2006). Recent research on ‘social-ecological’ systems has helped to both capture and understand some of this complexity and has begun to develop common frameworks for integrating knowledge (Cinner et al., 2009; Ostrom, 2009). However, simulation models, which are useful tools for understanding complex systems (Aumann, 2007), are relatively underutilised in social-ecological research and integrated environmental management.

Approaches to modelling social-ecological systems

Only a limited number of published simulation models couple biophysical and socioeconomic dynamics for coral reef systems. Existing models deal mostly with fisheries management (e.g. Gribble, 2003; Little et al., 2007; Shafer, 2007), although Gray et al.’s (2006) model also includes major industries such as shipping, oil and gas production and salt extraction. The general approach to building these models has been to develop ecological and socioeconomic (or resource exploitation) ‘modules’ that interact as part of the full social-ecological system. This has the dual advantages of drawing on expertise from different disciplines in the development of separate modules, and fostering transdisciplinary approaches to the definition of interactions between modules. The coupled systems developed by Gribble (2003), Little et al. (2007) and Gray et al. (2006) apply for coastal systems in Australia, while Shafer’s (2007) model is for reef dynamics in Hawaii. Given that the majority of people that depend on reef systems live in developing countries, and not in developed nations like Australia and the United States (Cesar et al., 2003), research to create (social-ecological) decision support tools for reef managers in developing countries is an important and urgent challenge.

Here, we demonstrate an approach to coupling biophysical and socioeconomic models for coral reefs in the Mexican state of Quintana Roo. These models have been developed separately using different platforms and have likewise been calibrated and validated separately (Perez et al., 2009; Melbourne-Thomas et al., in press). The biophysical model, CORSET (Coral Reef Scenario Evaluation Tool) applies for reefs off the Caribbean coasts of Mexico, Belize and Honduras, while the socioeconomic model (SimReef) describes dynamics specific to Quintana Roo. In the following sections we discuss management issues facing reefs in Quintana Roo and give brief descriptions of SimReef and CORSET. We then describe our step-wise approach to coupling the models and assess

the behaviour of the coupled system by comparing model outputs with empirical data and examining changes in coral cover under hypothetical scenarios for increases in the number of tourists visiting the region. We demonstrate that separate modelling tools can be integrated successfully, and urge that informed management of coral reefs in the future will utilise tools of this kind.

5.2 Coral reefs in Quintana Roo

The Mexican state of Quintana Roo occupies the eastern portion of the Yucatan Peninsula (Figure 5.1). Fringing reef systems extend along the mainland coast and around the Island of Cozumel, and the state also includes the offshore atoll of Banco Chinchorro (Figure 5.1B). These reefs provide important ecosystem services for coastal populations in Quintana Roo; they protect the coast from erosion, moderate the damaging effects of hurricanes, sustain subsistence and commercial fisheries, supply sand for beaches, and generate recreational opportunities (Cinner and Pollnac, 2004). Recent census data indicate a population of over one million, and annual tourist visitations in the order of eight million (SEIGE, 2010, Turismo). Demographic growth over the last 30 years (mainly as migration from neighbouring states) has been fuelled by a rapid growth in tourist numbers (Daltabuit et al., 2006). There is a high concentration of tourist resorts in the northern part of the Quintana Roo coast from Cancun to Playa del Carmen on the mainland, and on the island of Cozumel (Figure 5.1), and coastal development is rapidly extending southward (Jordán-Dahlgren and Rodríguez-Martínez, 2003). The construction of hotels close to the coast has resulted in increased sedimentation, which has negative consequences for reef health (Murray, 2007). Furthermore, waste-water and sewage from resorts and urban areas are generally untreated and are likely to have impacted coral reefs in the region (Murray, 2007), particularly given that the transport of liquid wastes is facilitated by the highly porous karst geology of the Yucatan Peninsula (Perry et al., 2009).

Coral reefs in Quintana Roo have been subject to intense artisanal fishing since the 1960s (Burke et al., 2004) and overexploitation of fishing resources is considered to be an important environmental impact in the region (Zárate Lomelí et al., 1999). Key fisheries are the Caribbean spiny lobster (*Panuliris argus*), reef fish and sharks, and these fisheries are commonly managed by fishing cooperatives that may have concessions to fish within protected areas such as the Puerto Morelos marine protected area (Rodríguez-Martínez, 2008) and the Sian Ka'an Biosphere Reserve (Arias-González et al., 2004). The queen conch (*Strombus gigas*) fishery has traditional significance in Quintana Roo, but its deterioration has been such that now it is fished only at Banco Chinchorro and Cozumel (Arenas Fuentes and Jiménez Badillo, 2007). Chronic stressors in the form of over-fishing and pollution from coastal development are likely to reduce the resilience of reef systems to disturbances such as hurricanes and coral bleaching events. This effect has been demonstrated for reefs in Belize and Honduras through the use of coral growth records (Carilli et al., 2009a). Reduced resilience is of particular concern given projected increases in the frequency of intense Atlantic hurricanes and coral bleaching events in coming decades (Donner, 2009; Bender et al., 2010). Local-scale, community-oriented programs for sustainable management of reef resources have been documented for Quintana Roo (Rodríguez-Martínez, 2008), but Mexico has no integrated coastal management programs at regional or national scales (Bezaury-Creel, 2005).

Previous modelling efforts for the human-environment system in Quintana Roo have examined future scenarios for population growth, tourism and land-use change (Lutz et al., 2000). However, these models are not integrated and have not been calibrated or validated, so are limited to exploratory and educational applications. Ecological modelling studies for the region (Arias-González, 1998; Arias-González et al., 2004) used non-spatial Ecopath platforms to examine differences in trophic structure between protected and non-protected areas. There is a need for tools that encapsulate the complex social-ecological drivers for the Quintana Roo reef system in a spatially-explicit manner. Such tools would be better placed to assist managers in evaluating regional-scale coral reef management options.

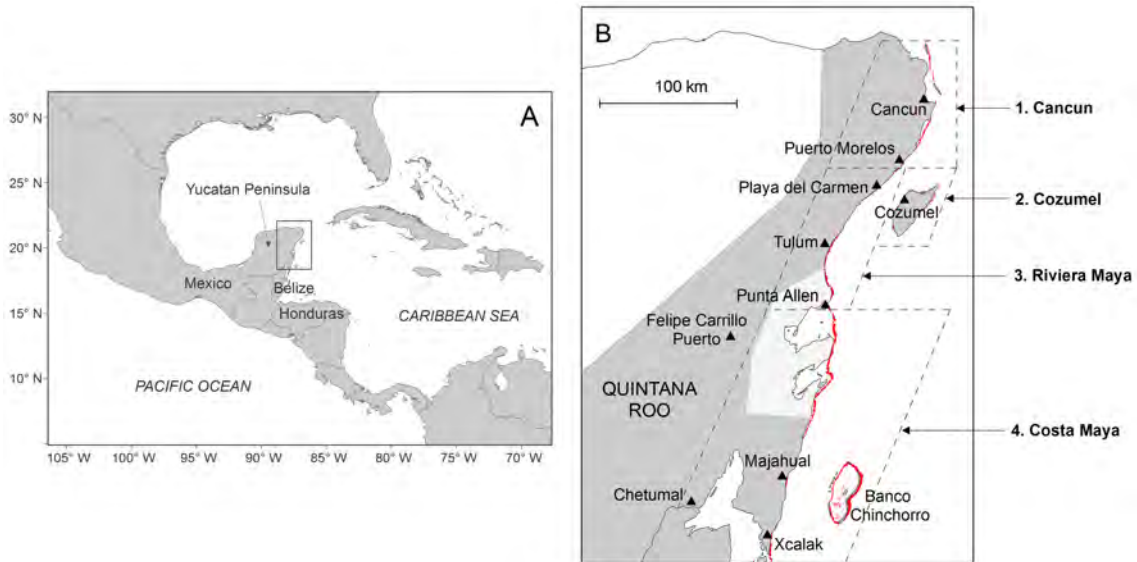


Figure 5.1: Maps indicating the location and spatial extent of the model region, with the Mexican state of Quintana Roo shaded in dark grey in (B). The location of coral reefs is indicated in red and includes both fringing reefs and the offshore atoll of Banco Chinchorro. The Sian Ka'an Biosphere Reserve, which is the largest protected area in Quintana Roo, is indicated in light grey (between Tulum and Majahual). Dashed lines delineate the four municipalities used in the coupled model.

5.3 SimReef: a socioeconomic model for the Quintana Roo coastal system

SimReef is an agent-based modeling tool that was developed for the Quintana Roo coastal system by Perez et al. (2009). The model simulates socioeconomic processes that affect reef function, and local experts and stakeholders participated interactively in the design phase. SimReef is implemented in the SmallTalk language of the Cormas platform (Bousquet et al., 1998), using the open source object-oriented program VisualWorks (Cincom Systems, Cincinnati, Ohio, USA) NonCommercial v7.6. The model is structured around four components: (i) fisheries, (ii) tourism, (iii) urbanization and (iv) reef ecology. Components (i) – (iii) are modeled at the scale of ‘economic development areas’ which correspond approximately with the four municipalities identified in Figure 5.1B, while reef ecology is modeled at the scale of reef cells (each with an area of approximately 25 km²). SimReef uses a gridded base-map which identifies the location of resorts, urban areas, and different habitat types (Figure 5.2A). The base-map is geographically distorted to emphasize areas of ecological and touristic importance. It includes recognizable features of the Quintana Roo region, namely: major cities, Mayan sites, the island of Cozumel, the offshore atoll Banco Chinchorro and the Sian Ka’an Biosphere Reserve. The model has been validated against population growth data for economic development areas of Quintana Roo (Cancun, Cozumel, Riviera Maya and Costa Maya) for the period 1994-2005 (Perez et al., 2009). SimReef’s predictions for population growth are a good match with census data, particularly for the two northern economic development areas where tourism growth has been most rapid (Cancun and Cozumel), but the validation approach used by Perez et al. (2009) is limited in that the calibration data set was also used for validation.

The fisheries component of SimReef models fishing activity for coastal vessels (1-2 fishers on board), high sea trawlers and prawn trawlers (5-10 fishers on board). A simple micro-economic model calculates vessel incomes on a monthly basis using seasonal average catches and approximate market prices for fish, prawns and lobsters (SEIGE, 2010, Pesca). Fishing fleets (comprising 10 vessels) assess the seasonal profitability of their fishing grounds and can select alternative fishing areas based on previous catches. Fleets are declared bankrupt when they are unable to meet salary costs over a one-year period. The tourism component of the model simulates resort development and job creation based on the flow of tourists entering Quintana Roo. Tourist flow is modeled using historical monthly tourism figures (SEIGE, 2010, Turismo), and so is effectively a forcing variable. This component resolves different categories of resorts, i.e. one-, three- and five-star resorts, with higher employment capacities and environmental impacts for higher category resorts (Álvarez Gil et al., 2001). The relationship between environmental impact and resort size and quality is a problematic one, as research suggests that larger, better quality chain hotels tend to have better environmental management systems (Álvarez Gil et al., 2001). However, the overall resource consumption, and therefore the impact on reefs stemming from activities such as construction and waste water flows, will still generally be greater from larger hotels of a higher standard (Bohdanowicz and Martinac, 2007).

The urbanization component of SimReef assumes a direct link between employment levels in the tourism industry and population growth; this relationship is broadly supported by census and employment data for Quintana Roo (SEIGE, 2010, Población, Turismo). Urban areas expand ad-

adjacent to resort areas and are assumed to have an environmental impact correlated with population size. The environmental impact of resorts and urban areas is represented in the model by means of a simple ‘environmental impact index’ derived from the number of resorts and the extent of urban areas in each economic development area. Finally, the reef ecology component of SimReef uses a highly simplified representation of local-scale ecological dynamics to model changes in coral cover, algal cover, herbivorous fish biomass and piscivorous fish biomass. Fishing activity depletes herbivorous and piscivorous fish stocks (up to the maximum expected biomass for fish catches from SEIGE, 2010, Pesca, depending on what biomass is available in a particular reef cell), and fishermen are presumed to target piscivorous fish preferentially (Pauly et al., 1998). Lobsters and prawns are not included in the reef ecology component; they act as passive stocks that are depleted by fishing activity (again determined directly by expected catches from SEIGE, 2010, Pesca) and have a certain probability of regeneration. SimReef’s environmental impact index has no effect on local-scale ecological processes.

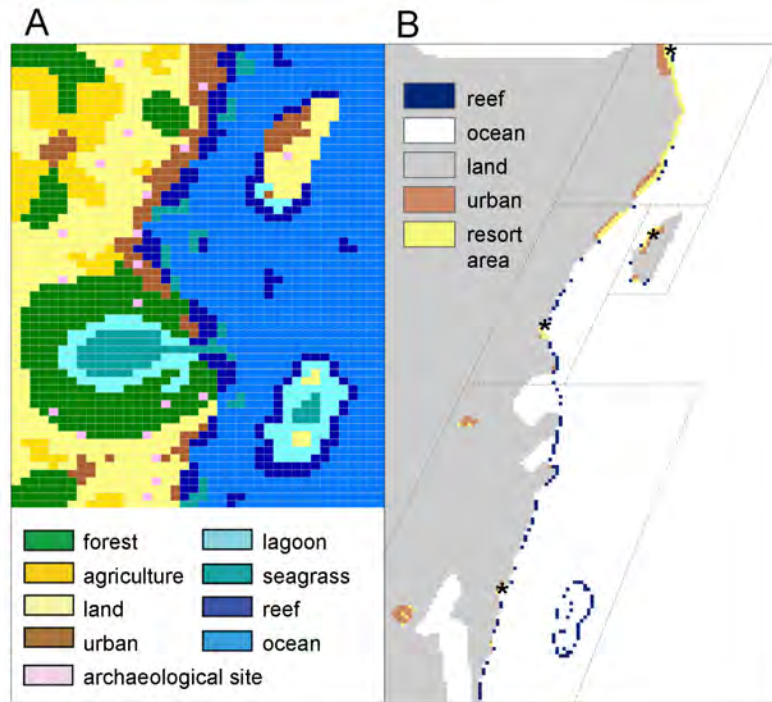


Figure 5.2: Gridded basemaps for (A) SimReef and (B) the coupled model. The SimReef base-map is geographically distorted but includes recognizable features of the Quintana Roo region (e.g. Cozumel to the north and Banco Chinchorro to the south). The base-map for the coupled model provides a more realistic spatial representation of the region with the location of coral reef cells extracted from reef distribution maps from the University of South Florida’s Institute for Marine Remote Sensing Millennium Coral Reef Mapping Project (IMaRS, 2004). Asterisks in (B) identify the locations of major ports for fishing vessels, while dashed lines delineate the four municipalities used in the coupled model. Cell dimensions are not explicit in the SimReef base-map, but each cell corresponds to an area of approximately 25 km^2 . The base-map for the coupled model uses a grid of $2 \text{ km} \times 2 \text{ km}$ cells.

5.4 CORSET: a multi-scale biophysical model for Mexican Caribbean reefs

CORSET (Coral Reef Scenario Evaluation Tool) is a multi-scale simulation model for a general coral reef system (Melbourne-Thomas et al., 2010, in press). Local-scale ecological dynamics are represented using mean-field equations (see Appendix A), and these dynamics are coupled across regional scales by larval dispersal. CORSET uses a ‘functional group’ approach to model interactions between two types of corals (brooding and broadcast spawning species), two types of algae (fleshy and foliose macroalgae, and turf algae), herbivorous fish, small-to-intermediate sized piscivorous fish, large piscivorous fish and sea urchins (Table 1.1 Chapter 1). Benthic covers of coral and algae, and the biomasses of fish and urchins are modelled in each reef cell of a gridded base-map using a weekly time step. Parameters that describe local-scale ecological processes are selected at random from predefined ranges (see Appendix A) derived from empirical observations. Parameter values vary between simulation years and between reef cells so that CORSET is stochastic. The model includes representations of ‘natural’ disturbances (hurricanes and disease), broad-scale anthropogenic impacts (coral bleaching events) and direct human impacts (harvesting, nutrification and sedimentation). CORSET is implemented in the open source object-oriented Python Programming Language (Python Software Foundation, Hampton, New Hampshire, USA) version 2.5. A version of the model for the Meso-American Reef system – incorporating coral reefs off the coasts of Mexico (Quintana Roo), Belize and Honduras – has been validated for the period 1980-2009 (Chapter 1).

5.5 Model coupling

Our general approach to coupling SimReef and CORSET was to replace the simplified ecological dynamics in SimReef with the more complex (and realistic) biophysical dynamics described by CORSET. Because the models differ in extent, spatial resolution (SimReef does not have explicit cell dimensions) and updating time step, the model coupling required modifications to both models, and spatial and temporal synchronisation of the models. The crux of the coupling was the definition of information flows and feedbacks between socioeconomic and biophysical ‘modules’. These steps are described in the following sections together with a brief discussion of external drivers for the coupled system and a preliminary assessment of model behaviour.

Modifications to SimReef and CORSET

To achieve compatibility between the socioeconomic and biophysical models we made two modifications to SimReef and two modifications to CORSET. The first modification to SimReef was to translate the model into Python (the language in which CORSET is implemented). We chose to translate SimReef, rather than integrating models based on different platforms (as in Villa and Costanza, 2000), for two reasons, namely that Python is object-oriented and so is an appropriate language for agent-based models such as SimReef, and because the effort of synchronising the two models developed on different platforms would have outweighed the effort required to translate SimReef. Translation had the added advantage of enabling us to make a second modification to

SimReef during the translation process, in that we removed high-seas fleet dynamics in the translated version since these do not relate to coral reef dynamics which are the focus of the coupled system. We also assumed a limit to the distance travelled by vessels in the coastal fleet of 100 km per fishing trip. This did not involve a modification to the model structure but this limit was not included in the original version of SimReef. It is a more realistic assumption than allowing vessels to fish over the entire region, given that each vessel must return to its home port and the duration of fishing trips will be limited by the amount of fuel which can be carried.

The two modifications made to CORSET were to add population dynamics for spiny lobsters (*Panulirus argus*), and modify the larval dispersal scheme. Lobster catches account for approximately two thirds of the total fisheries profits for Quintana Roo (INEGI, 2005), and so are clearly an important component of the socioeconomic system for this region (even though, as a functional group, lobsters do not play an ecologically prominent role). We introduced the following equation for lobster population dynamics into CORSET:

$$\frac{dL}{dt} = r_L L \left(1 - \frac{L}{k_L}\right) - d_L L + l_L - f_L, \quad (5.1)$$

where $\frac{dL}{dt}$ is the rate of change in lobster biomass L (in kg/km²). The parameter r_L is the intrinsic growth rate for lobster biomass = 0.335 yr⁻¹ and $k_L = 700$ kg/km² is the carrying capacity for lobster populations (FAO, 2003). The growth of lobsters might have been modelled in discrete steps, reflecting the moulting process of arthropods (as in Butler et al., 2005) but this approach was considered too detailed for the purposes of the coupled model for Quintana Roo. Lobster mortality rate was derived from the 2005 Southeast US Spiny Lobster Stock assessment report (SEDAR, 2005); $d_L = 0.3\text{--}0.4$ yr⁻¹. Published estimates are not available for the recruitment rate of one year old lobster post-larvae (l_L), but we derived a theoretical range for this parameter based on published values for mean monthly settlement density (0.041 settlers/m² for reefs in Florida; Butler et al., 2001) and the weight of year-old lobster recruits (Chávez, 2001). By assuming settlement densities $\pm 50\%$ of the value reported by Butler et al. (2001) and an estimate of between 96-99% post-settlement mortality from the same study, we estimated a theoretical range for $l_L = 0 - 6 \times 10^3$ kg km⁻² yr⁻¹ (the lower bound of this range was extended to zero to account for the possibility of recruitment failure for particular localities). We assumed that lobster recruitment is not dependent on local stocks, i.e. no L multiplier is included for the l_L parameter in Equation 5.1. This reflects the very long dispersal period of *P. argus* larvae (an average of 174 days; Goldstein et al., 2008) which means that local-scale self-recruitment is likely to be low. Finally, f_L is the fishing pressure on lobsters, which is dynamically derived from the socioeconomic module of the coupled model. The modified version of CORSET uses a discrete-time version of Equation 5.1, which is derived using the Euler method.

The second modification to CORSET was to adjust the larval dispersal scheme to represent larval connectivity between coral reef locations in Quintana Roo, rather than for the whole of the Meso-American Reef system (including Belize and Honduras). Larval dispersal is represented in CORSET by larval connectivity matrices which describe transition probabilities for larvae originating in each reef cell reaching (and settling in) every other reef cell in the model domain. These probabilities are derived from sophisticated larval transport simulations that consider both hydro-

dynamics and larval behaviour (Paris et al., 2007). Connectivity matrices are derived separately for corals (broadcast spawning species only), fish and sea urchins. We modified connectivity matrices to include transition probabilities between reef locations in Quintana Roo only. However, given that reefs in neighbouring Belize, and to a lesser extent Honduras, can act as larval sources for Quintana Roo reefs (see Chapter 1), we included a fixed larval supply from these ‘external’ sources by assuming uniform values for coral cover, fish biomass and urchin biomass on Belizean and Honduran reefs (derived as the average of reef state for reef cells in the Quintana Roo model domain at each time step). This approach was used previously in a separate version of CORSET for reefs in the Philippines region of the South China Sea (Chapter 4) and is adopted here for simplicity. The sensitivity of the model system to alternative assumptions about reef state in external sources is worthy of attention in more detailed evaluations of the behaviour of the coupled model beyond those presented here. A connectivity matrix for lobster larvae was not included as information on connectivity patterns for spiny lobster in the Meso-American region is not currently available and these patterns are most likely very different to those for coral, urchin and fish larvae due to the protracted dispersal period of *P. argus* larvae. Lobster recruitment varies randomly within the derived range $0 - 6 \times 10^3 \text{ kg km}^{-2} \text{ yr}^{-1}$ (i.e. assuming a uniform distribution) between reef cells and simulation years in the coupled model.

Synchronising the models

Modified versions of SimReef and CORSET were synchronised by means of a common base-map (spatial synchronisation) and time step (temporal synchronisation). The revised base-map for the coupled model is spatially realistic and the location of reef cells is geographically correct (Figure 5.2B). This map comprises a $2 \text{ km} \times 2 \text{ km}$ grid that is divided into four ‘municipalities’ which replace the economic development areas used in SimReef. Temporal synchronisation of the models did not require the biophysical and socioeconomic modules to use a common time step; biophysical dynamics in the coupled model are updated every week (as in CORSET) and socioeconomic dynamics use a monthly time step (as in SimReef). Information is passed between the two modules every month, and coupled model output is recorded for each year. Because CORSET is stochastic, the coupled model is also stochastic. In the following section we discuss the nature of information flows between socioeconomic and biophysical modules of the coupled model.

Defining information flows and feedbacks

The primary information flows between the biophysical and socioeconomic modules of the coupled model are summarised in Figure 5.3. Tourist resorts and urban areas affect water quality which is a driver for coral and algal cover. Decreased water quality is modelled using a ‘pollution index’ based on the environmental impact index in SimReef. The pollution index for each reef cell is based on the pollution value for the nearest resort or urban cell, where pollution value = 1.0 for three-star resorts, 3.0 for five-star resorts and 5.0 for urban cells. The assignment of these values is arbitrary (as in Perez et al., 2009), but is based on the assumption that larger resorts of a higher standard will generally have a greater impact on water quality than smaller, low quality resorts (Bohdanowicz and Martinac, 2007), and that the pollution impact will be highest for urban

areas. Pollution values scale inversely with the straight line distance (in number of cells) from the pollution source to each reef cell. Cells for which the scaled pollution index is > 0.5 are assumed to be subject to nutrification and sedimentation impacts. These impacts are detailed in Chapter 1 (Table 1.3) and act to decrease coral growth and recruitment while increasing coral mortality and the growth rate of macroalgae.

Harvesting of lobsters, herbivorous fish and piscivorous fish is based on fleet dynamics as in SimReef, with fishing pressure resulting in a direct reduction in fish and lobster biomasses. Fleet dynamics are modelled at the scale of municipalities, with one major port for each municipality (Figure 5.2B). The coupled model includes a feedback for fishing activity where fleet dynamics affect fish and lobster stocks which in turn determine fisher behaviour (i.e. the selection of fishing grounds). As in SimReef, a fleet can go bankrupt if its income is insufficient to pay wages. The current version of the coupled model does not include a feedback between the tourism industry and reef state, i.e. an ‘unhealthy’ reef with low coral cover and high algal biomass has no effect on tourist visitations. This assumption is reasonable for short term projections because the state of beaches and, to a lesser extent, the availability of archaeological sites are sufficient to attract tourists even if coral reefs are less appealing for SCUBA divers and snorkellers because of low coral cover (Torres, 2002). In the longer term, poor water quality may affect the state of beaches and so result in a decline in the tourism industry. However, this longer term feedback is difficult to model because of a lack of information regarding pollutant levels that result in degraded beaches and the magnitude of declines in tourist numbers precipitated by such degradation.

External drivers

External drivers for the coupled model (asterisked in Figure 5.3) are tourist flow, hydrodynamics and disturbance. As in SimReef, tourist flow is modelled using annual tourism figures which in turn drive resort development, population growth and urbanisation. Hydrodynamics is an indirect driver for the biophysical module of the coupled model in that larval connectivity is derived from particle tracking simulations that incorporate complex hydrodynamic features. Chapter 1 demonstrates how larval connectivity drives emergent spatial variation in reef community structure in CORSET, and this variability will have consequences for the behaviour and success of fishing fleets in the coupled model. Like CORSET, the coupled model enables simulation of disturbance events, namely hurricanes, coral bleaching and coral disease events. These disturbances act to reduce coral cover which has a flow-on effect for fish recruitment, and hence can also influence the success of fishing fleets in the coupled model. The current version of the coupled model does not include the effects of hurricanes on resorts and urban areas (as this was not a focus question for the original version of SimReef). However, given that hurricane damage to coastal areas has been an important socioeconomic driver for Quintana Roo in the past (e.g. the impacts of Hurricane Wilma; SourceMex, 2005), future versions of the coupled model will include the effects of hurricanes on resorts and urban areas. We note that the disturbance driver in the coupled model does not include direct damage to coral reef habitats from anchors or from SCUBA divers and snorkellers as these effects are assumed to be localised; they occur at scales smaller than our $2\text{ km} \times 2\text{ km}$ grid. No information is available about the cumulative impacts from direct damage that may manifest at larger spatial scales.

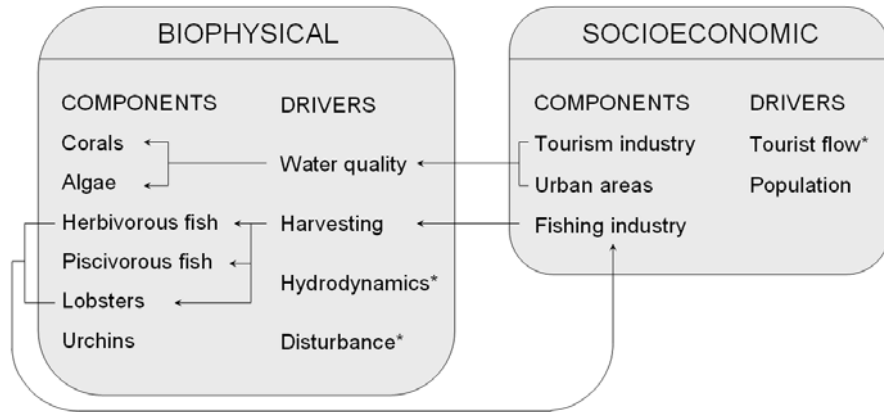


Figure 5.3: Coupled model components and drivers. Key information flows between socioeconomic and biophysical modules are indicated by arrows. Tourism flow, hydrodynamics and disturbance (asterisked) act as external drivers.

Preliminary assessment of model behaviour

We used two approaches to assess the general behaviour of the coupled system:

- (i) A comparison of model output with empirical values; and
- (ii) An evaluation of model responses under hypothetical scenarios for future changes in the tourism industry in Quintana Roo.

In the first approach we compared average simulation end points from 10 Monte Carlo model runs (each covering an 11-year simulation period from 1994-2005) with catch estimates derived from fisheries statistics for Quintana Roo in 2005 (from Mexico's National Institute of Statistics and Geography; INEGI, 2005). We also compared modelled values for coral cover, algal cover, herbivorous fish biomass and piscivorous fish biomass with published values for sites in Quintana Roo from ecological surveys in 2004-2005 (García-Salgado et al., 2006). There was reasonable correspondence between modelled values and empirical ranges for the variables we examined (Table 5.1). Modelled catches for fish and lobsters were slightly lower than empirical values derived from fishery statistics, however we note that, at least in the case of fish catches, derived values include catches from high seas fleets (which are not included in the coupled model) and so are likely to be over-estimates. Model estimates for algal cover in Quintana Roo were higher than values reported in García-Salgado et al. (2006) for 2004-2005. However, observations of algal covers across the region in 1999-2000 indicate values between 14% and 84% which is in better accordance with model outputs. Our findings under approach (i) demonstrate that the coupled system behaves reasonably in predicting general reef state and fish and lobster catches over multiple runs with the current parameter set. Further approaches to model validation are described in Section 5.6.

Table 5.1: Preliminary assessment of the behaviour of the coupled model for Quintana Roo. Model output represents average end points from 10 Monte Carlo model runs (each covering an 11-year simulation period from 1994-2005). Socioeconomic variables refer to the sum of fish and lobster catches for the four municipalities (Cancun, Cozumel, Riviera Maya and Costa Maya), while biophysical variables are minimum-maximum ranges across municipalities. Empirical values for fish and lobster catches are estimates based on fisheries statistics for Quintana Roo in 2005 (INEGI, 2005). Empirical values for biophysical variables are based on minimum-maximum ranges from ecological surveys in 2004-2005 (García-Salgado et al., 2006).

	Model output	Empirical values
Socioeconomic variables		
Fish catch (t)	740 – 1390	1500
Lobster catch (t)	150 – 190	200
Biophysical variables		
Coral cover (%)	9 – 30	8 – 40
Algal cover (%)	50 – 80	0 – 57
Herbivorous fish biomass (g/m ²)	10 – 50	9 – 54
Piscivorous fish biomass (g/m ²)	0 – 17	0 – 31

In our second approach to evaluating the behaviour of the coupled system we constructed hypothetical scenarios of increasing tourist numbers in Quintana Roo over a 10-year period. Census data for Quintana Roo indicate that annual tourist visitations increased by a factor of two over the period 1994-2005 (SEIGE, 2010, Turismo). The scenarios we examined assumed an increase in annual tourist visitations from the number of recorded visitations in 2005 to between one and five times the 2005 figure over a 10-year period. We used mean modelled coral cover in the four Quintana Roo municipalities as the response variable for these scenarios. Coral cover is expected to decrease under increased tourist visitations as high visitations drive increased hotel building and urban development in the model, both of which act as pollution sources for adjacent coral reefs. Our results indicate that in Cancun, which is already highly developed, there was no difference in average coral cover after 10 years between the ‘best-case’ scenario (where there is no further increase in tourist numbers) and the ‘worst-case’ scenario (where tourist numbers increase by a factor of five over the 10-year period; Figure 5.4). In contrast, there appears to be a threshold number of tourists that precipitate a drop in coral cover on reefs in Cozumel and Riviera Maya. Average modelled coral cover was highest on southerly reefs in Costa Maya, but declined steadily in this municipality between a 1.5-factor and 3.5-factor increase in tourist numbers. No additional loss of cover was apparent on reefs in Cozumel, Cancun and Costa Maya for more extreme scenarios (i.e. > 3.5 -factor increases in tourist numbers).

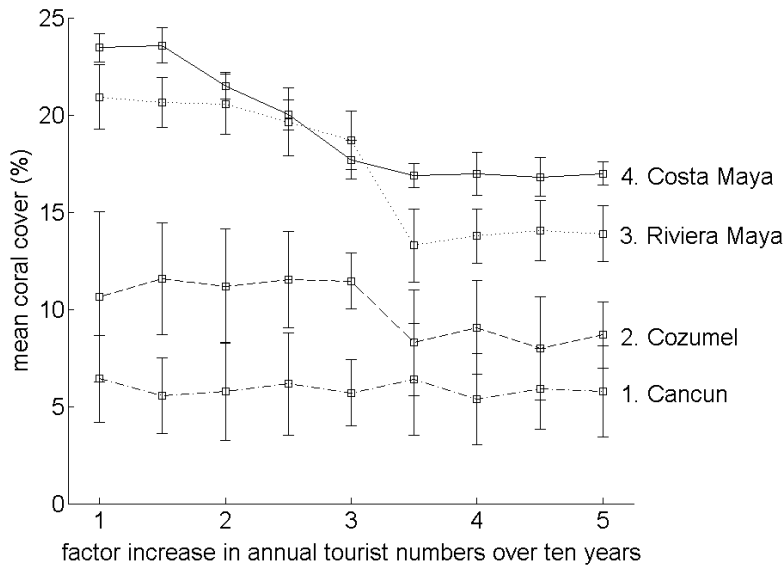


Figure 5.4: Average modelled coral cover in each of the four Quintana Roo municipalities under hypothetical scenarios for increasing tourist visitations. These scenarios assume increases in annual tourist visitation for the region by a factor of between one (i.e. no increase beyond the number of visitations in 2005) and five (i.e. five times 2005 visitations) over a 10-year period. Mean coral cover refers to the average cover for each municipality after 10 years. Error bars represent 95% confidence intervals from 10 Monte Carlo model runs.

5.6 Discussion

There is increasing recognition among both scientists and decision-makers of the complex, trans-disciplinary nature of environmental management problems. This complexity, combined with the need to consider social-ecological processes at multiple scales, is a key motivation for integrating different modelling approaches into higher-level simulation models (Villa and Costanza, 2000; van Delden et al., 2007). Here, we demonstrate an approach to coupling biophysical and socioeconomic models for coral reefs in the Mexican state of Quintana Roo. Our coupled system has applications for decision support in coral reef management and the approach itself can inform further attempts to couple dynamic models for human-environment systems.

Coupled models and coral reef management

Liu et al. (2007) synthesised results from six case studies from around the world to show that coupled systems exhibit a range of complex behaviours, including nonlinear dynamics, feedback loops and thresholds, that are not evident in single-discipline studies. However, there have been limited attempts to capture both biophysical and socioeconomic dynamics in simulation models for coral reef systems, and documented instances of coupled models are specific to reef systems in developed countries. The coupled system we have presented has the facility to capture social-ecological feedbacks that have implications for reef management in the Mexican state of Quintana Roo. Our hypothetical scenarios for increasing tourism development in this region demonstrate the utility of the coupled system in examining ecological responses to socioeconomic forcings, beyond the simplistic assumptions about increases in sedimentation and nutrification presented in Chapters 3 and 4.

Predicting the social-ecological impacts of the southward expansion of tourism development in Quintana Roo is a key concern for coastal management in the region (Bezaury et al., 1999) as is the continued pressure from extensive coastal development in the northern municipalities of Cancun and Cozumel. Forcing our coupled model system with increased tourist visitations over a 10-year simulation period suggests that tourism-driven coastal development alone is unlikely to result in further declines in coral cover on reefs near Cancun (Figure 5.4). However, model results indicate a threshold number of tourists that precipitate a loss of coral cover on reefs in the three other municipalities (Cozumel, Riviera May and Costa Maya). Tourism development appears to saturate at a certain level so that no further decreases in coral cover are evident in model projections where tourist numbers are greater than or equal to 3.5 times the number of visitations in 2005. We emphasise that our example scenarios are purely hypothetical; other socioeconomic and biophysical factors beyond raw tourist visitations are likely to influence trajectories for tourism development and ecological change in Quintana Roo in the future. Given additional threats to reef systems not examined in our hypothetical scenarios, such as increasing frequency and/or intensity of mass coral bleaching and hurricanes, the regulation of tourism development is likely to be a critical factor in maintaining reef ecosystem function in the region.

Limitations and recommendations for integrating models

Levins (1966) argues that models of biological populations must trade off generality, precision and realism because of the complexity of biological systems, and the same is certainly true for models of complex social-ecological systems. The degree of complexity included in a model will depend to a large extent on the question(s) which the model is intended to address and, as highlighted by Fulton et al. (2003), complexity introduced for the sake of completeness achieves nothing if the resulting model is not useful in the context it was designed for. Our discussion of limitations of our coupled model system for reefs in Quintana Roo relates to the issues of generality and complexity. At the end of this section we provide recommendations for where efforts might usefully be focused in future attempts to develop integrated models, based on the limitations of our coupled system.

Coupling SimReef and CORSET sacrifices generality; while CORSET is portable between different biogeographic regions as a stand-alone model (Chapter 4), the coupled system is specific to Quintana Roo. This is because the existing SimReef tool is region-specific. Unlike CORSET, SimReef was not designed to capture generic processes for reef-associated coastal systems in different parts of the world; tourism, population growth and fishing are modelled at the scale of municipalities and their representation in the model is particular to Quintana Roo. Achieving a portable social-ecological model framework for coral reef systems is a difficult task, particularly given the highly contextual nature of many socioeconomic processes. While the ecological processes that are fundamental to coral reef dynamics can be described by a generic model framework which applies for very different reefs around the world (as demonstrated in Chapters 1 and 4), socioeconomic processes are less amenable to such an approach. For example, “fishermen in Mexico and the Philippines may be very different social entities, with unrelated decision-making processes and dissimilar sets of values and beliefs” (Arias-González et al., in prep.). A portable framework for social-ecological systems must be capable of capturing such contextual differences.

In addressing complexity for the Quintana Roo reef system we have attempted to create a ‘minimum-realistic’ model (*sensu* Fulton et al., 2003) for social-ecological dynamics. However, some potentially important processes have been excluded, which we discuss separately for the socioeconomic and biophysical modules of the coupled system, as well as for the coupling mechanism itself. The socioeconomic module of the coupled system does not yet capture ‘switching’ of livelihoods between fishing and tourism industries. This is limiting because livelihood switching is likely to have occurred in Quintana Roo over the past 30 years, particularly in response to the tourism boom in the north of the state. However, data are not available to confirm whether fishermen left the fishing industry to take up construction and hospitality work in response to this boom. We also note that fuel costs to fishermen are not modelled, despite that this factor may influence fisher decisions about how far to travel to fishing grounds. In terms of the tourism industry, our model does not capture the negative social consequences of the growth in tourism for communities in Quintana Roo that are summarised by Murray (2007). Future versions of the model could potentially include some index of social welfare. Other socioeconomic components that could also be included in future versions of the model are cruise ships, conservation bodies, agriculture and construction industries, and patterns of investment in tourism development (as addressed in Kandelaars, 2000).

The biophysical module of the coupled system includes a simple representation of lobster population dynamics. While this is an improvement on the passive representation of lobster stocks in SimReef (where biomasses have a given probability of regeneration following harvesting), it requires further refinement. In particular, lobster recruitment could be modelled using data from transport simulations for spiny lobster larvae which are currently being conducted for the Meso-American region (M. J. Butler, pers. comm.). Other biophysical components that could be explored in future versions of the model include: (i) spawning aggregations for the Nassau grouper *Epinephelus striatus* (e.g. at Banco Chinchorro) that are important for the population dynamics of this commercial fish species but that are highly vulnerable to overfishing (Aguilar-Perera and Aguilar-Dávila, 1996; Heyman and Requena, 2003), and (ii) the role of nursery habitats, particularly mangrove forests, for coral reef fish species (Mumby et al., 2004). Finally, a key limitation of the coupled system in terms of the complexity of the coupling mechanism itself is the absence of feedbacks between reef state and the tourism industry. Such feedbacks are difficult to model in the absence of information about the degree to which ‘reef health’ is important to tourists. As indicated previously, this is not likely to be a problem for short-term projections, but may be an issue in making longer-term predictions about reef futures in the region.

In the light of these limitations we make the following recommendations for where efforts might usefully be focused in future attempts to couple biophysical and socioeconomic dynamics for coral reef systems:

- (i) An important knowledge gap in understanding and modelling socioeconomic dynamics relates to the factors which influence ‘livelihood switching’ in coastal communities, and the ways in which transitions between alternative livelihoods might be incorporated into simulation models. Cultural factors are often important in determining the willingness of stakeholders to change livelihoods (TNC, 2008; Cruz-Trinidad et al., 2009) and should be considered in models of socioeconomic dynamics.
- (ii) For regions such as Quintana Roo where the tourism industry is a critical component of the social-ecological system, there is a need for improved understanding of the feedbacks between ‘ecosystem health’ and tourism appeal. In particular, what level of environmental degradation will tourists tolerate in a given region or locality? and how does the behaviour of tourists influence degradation?
- (iii) Careful consideration should be given to the trade-offs between generality (or portability) and complexity in developing coupled biophysical-socioeconomic systems. Where the development of a portable model framework is an important consideration, methods need to be developed for accommodating contextual differences in socioeconomic processes between regions.

Next steps

Our demonstration of model coupling for the social-ecological coral reef system in Quintana Roo is the first step in a multi-stage process of model development, testing and refinement. The next steps in the process will involve: (i) a more detailed assessment of model behaviour over the time series 1994-2005 (results are presented here for a subset of model variables in 2005 only); (ii) model validation using an independent data set, e.g. for the period 2005-2009; and (iii) comparison of

different model formulations and sensitivity testing for key assumptions. Validation is complicated by limited data availability for the region; results from ecological surveys are sporadic in space and time and are not currently available for the period 2005-2008. Previous ecological surveys for reefs in Quintana Roo do not include observations of spiny lobster biomass. Similarly, limited socioeconomic data are available to validate simulated profits for the tourism and fisheries industries. The inclusion of additional socioeconomic and biophysical components discussed above is also limited by data availability. Nevertheless, testing alternative assumptions is an important component of model formulation (Grimm and Railsback, 2006) and can also help to identify critical knowledge gaps. We hope to make a tested version of our coupled model available to support decision making in coral reef management. Our approach can also be used to inform the development of an integrated, portable model framework that captures social-ecological processes which define coral reef systems.

Synthesis

A generic model framework for informing decision making in coral reef management

Threats to coral reef systems and the need for informed management approaches have been identified repeatedly throughout this thesis. Models are valuable tools for understanding reef responses to anthropogenic impacts and for informing decision making in reef management. The importance of a regional-scale approach to modelling and management is emphasised in Chapters 1 and 4; however, existing regional-scale models of reef systems are specific to particular geographic areas. CORSET (Coral Reef Scenario Evaluation Tool) is a dynamic simulation model that couples ecological processes from local to regional scales. It is the first regional-scale simulation model for coral reef ecosystems that has demonstrated utility for reef systems in different geographic regions. Instantiations of the model for the Meso-American Reef system (MAR; Chapter 1) and the Philippines/South China Sea region (PSCS; Chapter 4) demonstrate the validity of CORSET as a representation of coral reef dynamics and show that the model is portable between reef systems with different species assemblages and diversity characteristics, and that are subject to different stressors and disturbance regimes. CORSET can be used to inform regional- and subregional-scale decision making for coral reef management (Chapters 3 and 4).

Table S1 provides an evaluation of CORSET as a decision support tool against ‘internal’ criteria, i.e. desirable characteristics of models for decision support as outlined at the beginning of this thesis, and ‘external’ criteria derived from Sojda (2007) and Rizzoli and Young (1997). Sojda (2007) discusses the importance of verification (i.e. testing the internal logic of a model) and validation for decision support systems. Rizzoli and Young (1997) provide a set of desirable features of environmental decision support systems, but emphasise that many systems are successful without addressing all their prescribed characteristics. Listed characteristics that are relevant to dynamic systems (rather than knowledge-database type decision support systems) are incorporated into Table S1. These are: (i) model re-use and integration, (ii) the ability to deal with spatial data, and (iii) problem definition and solving (effectively ‘usability’ of a decision support system). CORSET performs well against internal and external criteria.

Table S1: Evaluation of CORSET as a decision support tool against internal criteria as outlined at the beginning of the thesis, and external criteria derived from Rizzoli and Young (1997) and Sojda (2007). Ticks (✓) and crosses (✗) indicate whether or not the model satisfies a given performance criterion. MAR = Meso-American Reef; PSCS = Philippines/South China Sea.

	Performance	Comments
1. Internal criteria		
Robust model framework	✓	The model framework has been tested through validation of the MAR and PSCS instantiations (Chapters 1 and 4) and sensitivity analysis for the MAR instantiation (Chapter 2). CORSET is also robust in that it behaves realistically for reef systems in different regions. Equations representing local-scale ecological processes (see Appendix A) have been tested extensively by Fung (2009) and are robust across a wide range of conditions.
Understandable inputs and components*	✓	The components and formulation of CORSET are reasonably understandable for non-experts. This will be improved by developing documentation that will be made available (together with example outputs) via a web portal.
Portability [†]	✓	This thesis demonstrates portability of CORSET by presenting instantiations for the MAR and PSCS regions. Portability to other reef systems depends to some extent on the availability of larval connectivity data, but as was indicated in Chapter 1, advances in hydrodynamic and particle-tracking modelling mean that connectivity information should soon become available for most, if not all reef systems.
Accessibility to end users*	✗	CORSET is not currently available publically, however a 'live' version will be made available in the near future via a web portal.
Bottom-up architecture	✓	Development of the model framework for CORSET has been bottom-up, i.e. based on the representation of fundamental ecological processes for coral reef systems. This means that complex behaviours are not pre-programmed in the model, but are emergent. A bottom-up approach is preferable to top-down architecture in terms of decision support, because top-down models are unable to capture complex behaviours that may occur in the future but have not yet been observed in real reef systems.

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	Performance	Comments
2. External criteria		
Verification of internal logic	✓	The ability of CORSET to realistically capture a 'healthy' reef state and to reproduce key processes typical of coral reefs in response to forcings provides verification of the internal logic of the model (this is also true of the the local-scale dynamic equations originally developed by Fung, 2009 – see Appendix A). Moreover the model has been developed and tested in collaboration with various experts who have confirmed the logic of the framework.
Validation	✓	Complementary approaches were used to validate the two instantiations of CORSET (Chapters 1 and 4). The model was able to reproduce coral reef communities typical of 'healthy' reefs in Meso-America and the Philippines, and to simulate past changes in reef state.
Ability to deal with spatial data	✓	CORSET is spatially explicit and is intended for the assessment of coral reef community dynamics at subregional to regional scales. The current version of the model uses gridded spatial data (for both inputs and outputs) and includes the facility to store simulation outputs in spatially referenced NetCDF (Network Common Data Form) format.

*These internal criteria cover the 'usability' criterion identified by Rizzoli and Young (1997).

†The internal portability criterion is equivalent to Rizzoli and Young's (1997) 'model re-use and integration' and criterion.

The implications of sensitivity and uncertainty for model performance

Sensitivity and uncertainty are issues for all ecological models used in a decision support context. The implications of sensitivity to parameter values and spatio-temporal resolution, and uncertainty in model formulation for the performance of the MAR instantiation of CORSET were evaluated in Chapter 2. An equivalent evaluation was not conducted for the Philippines instantiation of the model, but because the model framework is consistent across the two instantiations it is reasonable to assume that the findings from Chapter 2 are transferable to other instantiations of CORSET. Indeed, several of the local-scale ecological parameters in CORSET take the same values in both the MAR and PSCS instantiations of the model (Table A1, Appendix A) because data are not available to derive parameter values specific to particular regions. Validations of the two instantiations (in Chapters 1 and 4) suggest that consistency of some parameter values does not inhibit the model from replicating dynamics typical of a particular region. An alternative approach to simulating reef dynamics given limited information about parameter values for ecological processes is to use Bayesian Belief Networks (Wooldridge and Done, 2004; Wooldridge et al., 2005; Renken and Mumby, 2009). However, as was noted in Chapter 1, existing applications of Bayesian Belief Networks for coral reef systems are not spatially explicit.

The results of Chapter 2 indicate that model behaviour is sensitive to some key parameters, but that modelled community state is consistent across a range of spatial and temporal resolutions. Perhaps more important in terms of the use of CORSET as a decision support tool is that uncertainty in model formulation in relation to parameter variability in space and time affects the variability in model outcomes (Figures 2.10 and 2.11, Chapter 2). While this result is not particularly surprising, it emphasises the importance of matching assumptions to ecological or management questions. While the assumption of fixed parameter values across time steps in a particular model run (within a Monte Carlo set of simulations) enables the model user to examine the full spectrum of possible model behaviours, variation in parameter values between yearly time steps is a more realistic representation of what occurs in natural systems and so is more informative in terms of evaluating alternative management options. Uncertainty about the future impacts of human activities on coral reef systems (as opposed to uncertainty in model formulation) has implications for the predictability of reef state in the future. Scenario analysis is a useful approach for evaluating the predictability of reef futures under multiple, uncertain impacts.

Scenario analysis and reef futures under multiple impacts

The future of coral reef systems under multiple forms of anthropogenic stress and climate-related disturbance is uncertain. This poses a challenge to reef managers given that management decisions about when, where and how humans should act are generally founded on expectations for the future (Peterson et al., 2003). Scenarios are useful tools for exploring potential futures for ecological systems, and their use in coral reef research is increasing (e.g. Hoegh-Guldberg et al., 2007; Chang et al., 2008; Donner et al., 2009). By envisioning the likelihood of alternative futures under different management regimes, scenario analysis can help decision makers identify management approaches that will be robust across a range of potential future outcomes (Moss et al., 2010). Examples of

how CORSET can be used for scenario analysis were presented in Chapter 3 (for the MAR region) and Chapter 4 (for the PSCS region). Results of these analyses emphasise:

- (i) the role of multiple stressors in precipitating coral reef degradation (whether stressors act synergistically to reduce coral cover, as in Chapter 4, or preemptively to degrade coral reef community structure, as in Chapter 3),
- (ii) differences in predictability between reef systems that are subject to high levels of stress and disturbance (where modelled community composition tends to be more predictable) and ‘healthier’ reefs (where community composition tends to be less predictable), and
- (iii) the importance of larval connectivity in designing management strategies and prioritising locations for management actions.

Management priorities and available management levers differ substantially between the MAR and PSCS regions, and both of these factors are socioeconomic (rather than biophysical) in nature. Scenario analysis based only on biophysical dynamics is limited in the sense that it does not capture the bi-directional feedbacks between socioeconomic processes and ecological change. Accordingly, the example scenarios presented in Chapters 3 and 4 are restricted by assumptions about the nature of biophysical impacts, such as decreased fishing biomass through harvesting and inputs of nutrients and sediments, which are driven by patterns of human activity. These issues can be addressed by better integrating socioeconomic and biophysical dynamics in models of reef systems.

Towards integrated social-ecological model systems

There are very few examples of simulation models for coral reefs that couple biophysical and socioeconomic dynamics to form so-called ‘social-ecological’ systems. As was highlighted in Chapter 5, documented instances of coupled models are specific to reef systems in developed countries, i.e. Australia and the United States. Chapter 5 describes the process of integrating CORSET with a dynamic socioeconomic model for reef systems in the Mexican Caribbean. While this work is a useful demonstration of how the technicalities of model coupling can be overcome, the approach in this case is limited by a lack of data to formulate and parameterise complex feedbacks between socioeconomic and biophysical components of the coupled system. Furthermore, given the structure of the existing SimReef tool, the model coupling sacrifices the portability of CORSET so that the coupled system is not readily transferable from the Mexican case to other systems (although in principle a more generic socioeconomic module could be developed). A critical issue in attaining portability of social-ecological model frameworks is accommodating contextual differences in socioeconomic processes – such as differences in decision-making processes by stakeholders and the ways in which decisions are related to particular values and beliefs – between regions.

Future directions for CORSET

CORSET was designed to fulfil the functions of a research tool and a decision support tool for coral reef management. The performance of CORSET as a decision support tool according to

published criteria is evaluated in Table S1, but the real test of its applicability will be the value of the model to end-users. Results from scenario analysis using CORSET are available as a data CD (MDSWG, 2009) and online (www.reefutures.org). There is ongoing work to make a ‘live’ version of CORSET accessible to non-experts via a web portal. The model (together with detailed documentation on model structure, how to parameterise and run it, and example runs) will soon be available publically via the reefutures.org web portal and will be hosted by the University of Tasmania’s super computer facility (TPAC). In the first instance, users will have access to the Meso-American and Philippines versions of CORSET. In the longer term the web portal will facilitate the creation of new instantiations of the model for different reef systems, with input of parameters, base-maps and larval connectivity information by the user. CORSET is also being used to inform the development of a generic, portable framework for models of social-ecological reef systems. The development and implementation of such a framework will be an important step in the difficult journey towards sustainable management of coral reef resources.

Appendices

A. The local ecological model

The regional-scale biophysical model presented in this thesis (CORSET; Coral Reef Scenario Evaluation Tool) comprises multiple instantiations of a local-scale mean-field model of ecological dynamics (Fung, 2009) that are connected by larval transport (Figure 1.1, Chapter 1). The local model is defined by seven differential equations which have been parameterised using available data for shallow coral reef habitats (~ 5 m – 20 m depth). The CORSET implementation of the local-scale model distinguishes between brooding and spawning corals, so that the model system comprises eight differential equations (Equations A1 – A3 and A7 – A11). CORSET uses discrete-time (difference equations) approximations of these differential equations, which were derived using Euler’s method. Full details of the local-scale model formulation, its behaviour and derivations of generic parameter ranges are available in Fung (2009). The parameter ranges used in this thesis, which apply to the western Atlantic and the Indo-Pacific (Table A1), are derived using the same approach as in Fung (2009).

The variables followed in the model are the proportional covers of brooding corals (C_b), spawning corals (C_s), hard corals ($C = C_b + C_s$), macroturf (T), macroalgae (M) and grazed epilithic algal communities or EAC ($E = 1 - C_b - C_s - T_M$), and the biomasses of herbivorous fish (H), small-to-intermediate piscivorous fish (P_s), large piscivorous fish (P_l) and sea urchins (U).

The change in proportional cover of brooding corals (C_b) is given by

$$\frac{dC_b}{dt} = \underbrace{r_C(1 - \beta_M M)(E + \alpha_C T)C_b}_{\text{growth}} - \underbrace{d_C C_b}_{\text{mortality}} - \underbrace{\gamma_{MC} r_M M C_b}_{\text{macroalgal overgrowth}} + \underbrace{l_{C_b}(E + \epsilon_C T)}_{\text{recruitment}}, \quad (\text{A1})$$

where all parameters (r , β_M , α_C etc.) are defined in Table A1, as are all parameters used in the following equations. Similarly, for the proportional cover of spawning corals (C_s)

$$\frac{dC_s}{dt} = \underbrace{r_C(1 - \beta_M M)(E + \alpha_C T)C_s}_{\text{growth}} - \underbrace{d_C C_s}_{\text{mortality}} - \underbrace{\gamma_{MC} r_M M C_s}_{\text{macroalgal overgrowth}} + \underbrace{l_{C_s}(E + \epsilon_C T)}_{\text{recruitment}} \quad (\text{A2})$$

and macroturf (T)

$$\frac{dT}{dt} = \underbrace{\zeta_T(1 - \theta)E}_{\text{growth}} - \underbrace{g_T \theta T}_{\text{grazing}} - \underbrace{r_C \alpha_C(1 - \beta_M M)CT}_{\text{coral overgrowth}} - \underbrace{\gamma_{MT} r_M MT}_{\text{macroalgal overgrowth}} - \underbrace{\epsilon_C(l_{C_b} + l_{C_s})T}_{\text{coral recruitment}}, \quad (\text{A3})$$

where θ is the grazing term given by

$$\theta = \theta_H + \theta_U. \quad (\text{A4})$$

Grazing by herbivorous fish (θ_H) and sea urchins (θ_U) is scaled by competition between these two groups such that

$$\theta_H = \left(\frac{H}{i_H + H} \right) \left\{ 1 - \lambda_U \left(\frac{U}{i_U + U} \right) \right\}, \quad (\text{A5})$$

$$\theta_U = \left(\frac{U}{i_U + U} \right) \left\{ 1 - \lambda_H \left(\frac{H}{i_H + H} \right) \right\}. \quad (\text{A6})$$

The change in proportional cover of macroalgae (M) is given by

$$\frac{dM}{dt} = \underbrace{r_M M E}_{\text{growth over EAC}} - \underbrace{g_M \theta M}_{\text{grazing}} + \underbrace{\gamma_{MC} r_M M C}_{\text{growth over coral}} + \underbrace{\gamma_{MT} r_M M T}_{\text{growth over turf}} \quad (\text{A7})$$

and in the biomass of herbivorous fish (H) by

$$\begin{aligned} \frac{dH}{dt} = & \underbrace{\theta_H (g_M M \mu_M + g_T T \mu_T + \zeta_T E \mu_E)}_{\text{growth}} \\ & - \underbrace{\frac{d_H H}{\text{mortality}}}_{\text{mortality}} - \underbrace{(g_{P_s} P_s + g_{P_l} P_l) \left(\frac{H^2}{i_{PH}^2 + H^2} \right)}_{\text{predation}} - \underbrace{\rho_H f \left(\frac{H}{i_{FH} + H} \right)}_{\text{fishing}} + \underbrace{l_H}_{\text{recruitment}}. \end{aligned} \quad (\text{A8})$$

Similarly for the biomass of small-to-intermediate piscivorous fish (P_s)

$$\begin{aligned} \frac{dP_s}{dt} = & \underbrace{(1 - \phi_{P_s}) r_{P_s} g_{P_s} \left(\frac{H^2}{i_{PH}^2 + H^2} \right) P_s}_{\text{growth, including transition to large size class}} \\ & - \underbrace{\frac{d_{P_s} P_s}{\text{mortality}}}_{\text{mortality}} - \underbrace{\psi_{P_l} g_{P_l} \left(\frac{P_s^2}{i_{P_l P_s}^2 + P_s^2} \right) P_l}_{\text{predation}} - \underbrace{\rho_{P_s} f \left(\frac{P_s}{i_{FP_s} + P_s} \right)}_{\text{fishing}} + \underbrace{l_{P_s}}_{\text{recruitment}}, \end{aligned} \quad (\text{A9})$$

large piscivorous fish (P_l)

$$\begin{aligned} \frac{dP_l}{dt} = & \underbrace{\phi_{P_s} r_{P_s} g_{P_s} \left(\frac{H^2}{i_{PH}^2 + H^2} \right) P_s}_{\text{transition from smaller size class}} \\ & + \underbrace{r_{P_l} g_{P_l} \left\{ \left(\frac{H^2}{i_{PH}^2 + H^2} \right) + \psi_{P_l} \left(\frac{P_s^2}{i_{P_l P_s}^2 + P_s^2} \right) \right\} P_l}_{\text{growth}} - \underbrace{\frac{d_{P_l} P_l}{\text{mortality}}}_{\text{mortality}} - \underbrace{\rho_{P_l} f \left(\frac{P_l}{i_{FP_l} + P_l} \right)}_{\text{fishing}} \end{aligned} \quad (\text{A10})$$

and sea urchins (U)

$$\frac{dU}{dt} = \underbrace{\kappa_U \theta_U (g_M M \mu_M + g_T T \mu_T + \zeta_T E \mu_E)}_{\text{growth}} - \underbrace{d_U U - q_U U^2}_{\text{mortality}} + \underbrace{l_U}_{\text{recruitment}}. \quad (\text{A11})$$

Table A1: Local model parameter definitions and values derived for the western Atlantic and Indo-Pacific regions. The Meso-American instantiation of CORSET (Chapters 1, 2, 3 and 5) uses the parameter set for the western Atlantic, while the Philippines/South China Sea instantiation of the model (Chapter 4) uses parameters for the Indo-Pacific. Parameter values are derived using the same parameterisation methodology as detailed in Fung (2009). Mathematically derived parameter restrictions detailed in the footnotes are required to keep state variables within a realistic biological range, i.e. in the range 0 - 1 for benthic covers, and ≥ 0 (but not tending to infinity) for consumer biomasses (see Fung, 2009, for detailed derivations).

Parameter	Definition	Derived values western Atlantic	Derived values Indo-Pacific
Benthic parameters			
d_C	The background mortality rate of brooding and spawning corals	$0.02 - 0.1 \text{ yr}^{-1}$	$0.02 - 0.1 \text{ yr}^{-1}$
r_C	The growth rate of existing coral over grazed EAC	$0.04 - 0.2 \text{ yr}^{-1}$	$0.1 - 0.2 \text{ yr}^{-1}$
α_C	The growth rate of coral over macro turf, relative to its growth over grazed EAC	$0 - 1$	$0 - 1$
ϵ_C	The recruitment rate of coral onto macro turf, relative to the rate onto grazed EAC	$0.05 - 0.15$	$0.05 - 0.15$
$l_{C_b}, l_{C_s}^{(1)}$	The recruitment rates of brooding and spawning corals onto grazed EAC	Modelled separately	Modelled separately
g_T	The maximum rate (per unit of grazing pressure θ) at which existing macro turf is grazed down	$5 - 15 \text{ yr}^{-1}$	$5 - 15 \text{ yr}^{-1}$
ζ_T	The rate at which grazed EAC grows into macro turf	$2 - 20 \text{ yr}^{-1}$	$2 - 20 \text{ yr}^{-1}$
g_M	The maximum rate (per unit of grazing pressure θ) at which existing macroalgae is grazed down	$0.01 g_T - g_T \text{ yr}^{-1}$	$0.01 g_T - g_T \text{ yr}^{-1}$
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Parameter	Definition	Derived values western Atlantic	Derived values Indo-Pacific
r_M	The growth rate of macroalgae over grazed EAC	$0.05 - 0.4 \text{ yr}^{-1}$	$0.05 - 0.4 \text{ yr}^{-1}$
β_M	Coral growth is inhibited by the presence of nearby macroalgae and this is represented as depression of r_G by the factor $(1 - \beta_M M)$	$0.4 - 0.9 \text{ yr}^{-1}$	$0.2 - 0.3 \text{ yr}^{-1}$
γ_{MC}	The growth rate of macroalgae over coral, relative to its growth over grazed EAC	$0 - 0.9$	$0 - 0.9$
γ_{MT}	The growth rate of macroalgae over macroturf, relative to its growth over grazed EAC	$0 - 0.9$	$0 - 0.9$
Consumer parameters			
$i_H^{(2)}$	A parameter that measures the inaccessibility of algae (turf and macroalgae) to herbivorous fish grazing	$3 \times 10^3 - 5 \times 10^5 \text{ kg/km}^2$	$i_{Hmin} - 4 \times 10^5 \text{ kg/km}^2$
i_{PH}	A parameter that measures the inaccessibility of herbivorous fish to predation by piscivorous fish	$7 \times 10^3 - 1 \times 10^4 \text{ kg/km}^2$	$7 \times 10^3 - 1 \times 10^4 \text{ kg/km}^2$
i_{FH}	A parameter that measures the inaccessibility of herbivorous fish to fishermen	$7 \times 10^2 - 1 \times 10^3 \text{ kg/km}^2$	$7 \times 10^2 - 1 \times 10^3 \text{ kg/km}^2$
$d_H^{(3)}$	The death rate of herbivorous fish from all factors other than predation by piscivorous fish and fishing	$d_{Hmin} - 2 \text{ yr}^{-1}$	$d_{Hmin} - 5 \text{ yr}^{-1}$
$\mu_M, \mu_T, \mu_E^{(4)}$	The herbivorous fish biomass accumulated from grazing on 100% cover of macroalgae, macroturf and EAC respectively, and which contributes to somatic growth of herbivorous fish	$60 - \mu_{max} \text{ kg km}^{-2} \text{ yr}^{-1}$	$9 \times 10^2 - \mu_{max} \text{ kg km}^{-2} \text{ yr}^{-1}$
<i>continued on next page</i>			

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Parameter	Definition	Derived values western Atlantic	Derived values Indo-Pacific
ρ_H	The proportion of total fishing pressure f which acts on herbivorous fish ($\rho_H + \rho_{P_s} + \rho_{P_i} = 1$)	0 – 1	0 – 1
$l_H^{(1)}$	The recruitment rate of herbivorous fish	Modelled separately	Modelled separately
$i_{P_i P_s}$	A parameter that measures the inaccessibility of small-to-intermediate piscivorous fish to predation by large piscivorous fish	$7 \times 10^3 - 1 \times 10^4 \text{ kg/km}^2$	$7 \times 10^3 - 1 \times 10^4 \text{ kg/km}^2$
i_{FP_s}	A parameter that measures the inaccessibility of small-to-intermediate piscivorous fish to fishermen	$7 \times 10^2 - 1 \times 10^3 \text{ kg/km}^2$	$7 \times 10^2 - 1 \times 10^3 \text{ kg/km}^2$
$d_{P_s}^{(5)}$	The death rate of small-to-intermediate piscivorous fish from all factors other than predation and fishing	$d_{P_s \min} - 2 \text{ yr}^{-1}$	$d_{P_s \min} - 3 \text{ yr}^{-1}$
g_{P_s}	The maximum predation rate of small-to-intermediate piscivorous fish on herbivorous fish	1 – 2 yr^{-1}	1 – 2 yr^{-1}
r_{P_s}	The proportion of consumed biomass which is used for somatic growth, for small-to-intermediate piscivorous fish	0.035 – 0.105	0.07 – 0.1
ϕ_{P_s}	The proportion of small-to-intermediate piscivorous fish biomass that becomes large piscivorous fish biomass due to predation and subsequent growth	0 – 10	0 – 10
ρ_{P_s}	The proportion of total fishing pressure f which acts on small-to-intermediate piscivorous fish ($\rho_H + \rho_{P_s} + \rho_{P_i} = 1$)	0 – 1	0 – 1
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Parameter	Definition	Derived values western Atlantic Derived values Indo-Pacific
$l_{P_s}^{(1)}$	The recruitment rate of small-to-intermediate piscivorous fish	Modelled separately
i_{FP_I}	A parameter that measures the inaccessibility of large piscivorous fish to fishermen	$7 \times 10^2 - 1 \times 10^3 \text{ kg/km}^2$ $7 \times 10^2 - 1 \times 10^3 \text{ kg/km}^2$
$d_{P_I}^{(6)}$	The death rate of large piscivorous fish from all factors other than predation and fishing	$d_{P_{Imin}} - 0.9 \text{ yr}^{-1}$ $d_{P_{Imin}} - 1 \text{ yr}^{-1}$
g_{P_I}	The maximum predation rate of large piscivorous fish on herbivorous fish	$0.25 - 0.75 \text{ yr}^{-1}$ $0.25 - 0.75 \text{ yr}^{-1}$
r_{P_I}	The proportion of consumed biomass which is used for somatic growth, for large piscivorous fish	$0.03 - 0.09$ $0.03 - 0.045$
ψ_{P_I}	The predation rate on small-to-intermediate piscivorous fish by large piscivorous fish, relative to that on herbivorous fish	$2 - 4$ $2 - 4$
ρ_{P_I}	The proportion of total fishing pressure f which acts on large piscivorous fish ($\rho_H + \rho_{P_s} + \rho_{P_I} = 1$)	$0 - 1$ $0 - 1$
$f^{(7)}$	The maximum fishing biomass which can be caught	$0 - 5 \times 10^3 \text{ kg km}^{-2} \text{ yr}^{-1}$ $0 - 6 \times 10^4 \text{ kg km}^{-2} \text{ yr}^{-1}$
$d_U^{(8)}$	The death rate of urchins	$d_{Umin} - 1 \text{ yr}^{-1}$ $d_{Umin} - 0.6 \text{ yr}^{-1}$
$q_U^{(9)}$	Quadratic mortality of urchins	$1 \times 10^{-6} \text{ yr}^{-1}$ $1 \times 10^{-6} \text{ yr}^{-1}$
κ_U	A parameter that measures the biomass accumulated by urchin grazing and which contributes to somatic growth relative to that for herbivorous fish grazing	$1 - 10$ $1 - 10$
<i>continued on next page</i>		

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Parameter	Definition	Derived values western Atlantic	Derived values Indo-Pacific
$l_U^{(1)}$	The recruitment rate of urchins		
λ_H	A parameter that determines the competitiveness of herbivorous fish relative to urchins	Modelled separately $0.6 - 1$	Modelled separately $0.6 - 1$
λ_U	A parameter that determines the competitiveness of urchins relative to herbivorous fish	$1 - \lambda_H$	$1 - \lambda_H$
$i_U^{(10)}$	A parameter that measures the inaccessibility of algae (turf and macroalgae) to urchin grazing	$i_{Umin} - 3 \times 10^6 \text{ kg/km}^2$	$i_{Umin} - 2 \times 10^6 \text{ kg/km}^2$

⁽¹⁾ Recruitment terms ($l_C, l_{C_s}, l_H, l_{P_s}, l_U$) are modelled externally to the local model, based on matrices defining connectivity between reef cells as detailed in Chapters 1 and 4. Parameters used for modelling larval production and post-settlement processes are provided in Table B1, Appendix B.

⁽²⁾ Indo-Pacific: $i_{Hmin} = \max \left\{ 1000, \frac{900 \times \max\{g_T, \zeta_T\}}{5 - 0.000001} \right\}$.

⁽³⁾ W. Atlantic: $d_{Hmin} = \max \left\{ 0.2, \left(\frac{\mu \times \max\{g_T, \zeta_T\}}{i_H} + 0.000001 \right) \right\}$,

Indo-Pacific: $d_{Hmin} = \max \left\{ 0.3, \left(\frac{\mu \times \max\{g_T, \zeta_T\}}{i_H} + 0.000001 \right) \right\}$. Here, $\mu_M = \mu_T = \mu_E = \mu$.

⁽⁴⁾ W. Atlantic: $\mu_{max} = \min \{100000, \mu_{max1}\}$, where $\mu_{max1} = \min \left\{ \frac{i_H \times (2 - 0.000001)}{\max\{g_T, \zeta_T\}}, \frac{i_U \times (1 - 0.000001)}{\kappa_U \times \max\{g_T, \zeta_T\}} \right\}$,

Indo-Pacific: $\mu_{max} = \min \{500000, \mu_{max1}\}$, where $\mu_{max1} = \min \left\{ \frac{i_H \times (5 - 0.000001)}{\max\{g_T, \zeta_T\}}, \frac{i_U \times (0.6 - 0.000001)}{\kappa_U \times \max\{g_T, \zeta_T\}} \right\}$

⁽⁵⁾ $d_{P_smin} = \max \{0.2, (1 - \phi_{P_s}) r_{P_s} g_{P_s}\}$.

⁽⁶⁾ W. Atlantic: $d_{P_lmin} = r_{P_l} g_{P_l} (1 + \psi_{P_l}) + 0.000001$,

Indo-Pacific: $d_{P_lmin} = \max \{0.07, r_{P_l} g_{P_l} (1 + \psi_{P_l}) + 0.000001\}$.

(7) In scenario analysis f is treated as a forcing parameter, and can vary over time.

(8) W. Atlantic: $d_{Umin} = \max \left\{ 0.3, \frac{\kappa_U \times \mu \times \max\{g_T, \zeta_T\}}{i_U} + 0.000001 \right\},$

Indo-Pacific: $d_{Umin} = \max \left\{ 0.05, \frac{\kappa_U \times \mu \times \max\{g_T, \zeta_T\}}{i_U} + 0.000001 \right\}.$

(9) Quadratic mortality of sea urchins, q_U , is included in the regional implementation of the local ecological model to prevent uncontrolled population explosions in this functional group. This term is a proxy for consumption of sea urchins by fish and invertebrate predators (Randall et al., 1964; Harborne et al., 2009).

(10) W. Atlantic: $i_{Umin} = \max \left\{ 2000, \frac{60\kappa_U \times \max\{g_T, \zeta_T\}}{1-0.000001} \right\},$

Indo-Pacific: $i_{Umin} = \max \left\{ 2000, \frac{900\kappa_U \times \max\{g_T, \zeta_T\}}{1-0.000001} \right\}.$

B. Recruitment parameters

Table B1: Larval production and post-settlement parameters for the Meso-American and Philippines/South China Sea instantiations of CORSET (generic recruitment parameters apply to both regions). Details of derivations for these parameters are provided in the text of Appendix B.

Parameter	Derived value(s)	Sources
Meso-American Reef system		
Brooding and spawning coral larval production (at 100% cover)	$2 \times 10^9 - 6 \times 10^9 \text{ km}^{-2} \text{ yr}^{-1}$	1, 2, 3
Herbivorous fish larval production	$5 \times 10^3 - 7 \times 10^3 \text{ kg}^{-1} \text{ yr}^{-1}$	3, 4, 5
Small piscivorous fish larval production	$3 \times 10^2 - 5 \times 10^2 \text{ kg}^{-1} \text{ yr}^{-1}$	3, 4, 5
Large piscivorous fish larval production	$7 \times 10^2 - 9 \times 10^2 \text{ kg}^{-1} \text{ yr}^{-1}$	3, 4, 5
Urchin larval production	$6 \times 10^2 - 8 \times 10^2 \text{ kg}^{-1} \text{ yr}^{-1}$	3, 6, 7
Philippines/South China Sea region		
Brooding and spawning coral larval production (at 100% cover)	$8 \times 10^8 - 2 \times 10^9 \text{ km}^{-2} \text{ yr}^{-1}$	1, 2, 3
Herbivorous fish larval production	$5 \times 10^3 - 7 \times 10^3 \text{ kg}^{-1} \text{ yr}^{-1}$	3, 4, 5
Small piscivorous fish larval production	$1 \times 10^2 - 4 \times 10^2 \text{ kg}^{-1} \text{ yr}^{-1}$	3, 4, 5
Large piscivorous fish larval production	$1 \times 10^3 - 4 \times 10^3 \text{ kg}^{-1} \text{ yr}^{-1}$	3, 4, 5
Urchin larval production	$2 \times 10^5 - 4 \times 10^5 \text{ kg}^{-1} \text{ yr}^{-1}$	3, 6, 7
Generic		
Initial mortality of brooded coral larvae	0.7 – 0.99	8
Mortality of brooding and spawning coral recruits during the first year following settlement	0.2 – 0.7 yr^{-1}	9
Mortality of fish and urchin recruits during the first year following settlement	density dependent	10, 11, 12, 13
The area of 1yr old coral recruits	2.18 cm^2	14
The biomass of 1yr old herbivorous fish recruits	80 g	5
The biomass of 1yr old piscivorous fish recruits	150 g	5
The biomass of 1yr old urchin recruits	10 g	7, 15

Sources: ¹Harrison and Wallace (1990), ²Richmond (1988), ³(see text below), ⁴Cowen et al. (2006, supplementary material), ⁵Froese and Pauly (2004), ⁶Levitan (1991), ⁷Levitan (1988), ⁸Fadlallah (1983), ⁹Babcock (1985), ¹⁰Hixon and Webster (2002), ¹¹Anderson et al. (2007), ¹²Carr and Hixon (1995), ¹³Stimson (1990), ¹⁴Edmunds (2007), ¹⁵Carpenter (1997)

Larval production

Published estimates of larval production for corals, fish and sea urchins are sparse, variable and uncertain. Orders of magnitude for the numbers of larvae produced were estimated from available sources (Levitan, 1988; Richmond, 1988; Harrison and Wallace, 1990; Levitan, 1991; Froese and Pauly, 2004; Cowen et al., 2006), and then estimates were refined through a process of model tuning,

i.e. varying larval production (within acceptable ranges derived from the literature) to achieve coral cover and consumer biomasses representative of a healthy reef system. A healthy reef system is defined according to published indicator values (as indicated in Chapters 1 and 4). The practical steps involved in model tuning were to (i) run the model over long time series (50 – 100 years) using broad ranges for larval production parameters, (ii) compare model output with expected values for coral cover and consumer biomasses, and (iii) increase the minimum and decrease the maximum values for larval production parameters before re-running the model. This process was conducted separately for each of brooding and spawning corals, herbivorous, small piscivorous and large piscivorous fish. Larval production estimates derived using this method for the Meso-American Reef system and the Philippines/South China Sea region are reported in Table B1. Production over the course of a year is assumed to be equivalent for brooding and spawning corals (Richmond, 1988; Harrison and Wallace, 1990).

Pre- and post-settlement mortality are represented explicitly for brooded coral larvae. The estimate for pre-settlement mortality is 0.7 – 0.99, assuming that brooded larvae are competent to settle within an average period of 4 days (Fadlallah, 1983) and that average pre-settlement mortality is between 0.25 day⁻¹ (as for spawned coral larvae; Tables 1.2 and 4.2) and 0.7 day⁻¹ (as for post-settlement mortality of coral larvae; Table B1). Pre-settlement mortality is implicit in connectivity matrices for spawned coral, fish and urchin larvae.

Post-settlement processes

The post-settlement mortality rate of brooding and spawning coral recruits during the first year following settlement is 0.2 – 0.7 yr⁻¹ (Babcock, 1985). Mortality of fish and sea urchin recruits is set at a constant background level with density dependent mortality beyond a threshold of 1 recruit/m², based on findings from Jones (1990). Hixon and Webster (2002) present a regional-scale comparison of post-settlement mortality rates for a species of damselfish (*Pomacentrus moluccensis*) based on studies from the southern (Doherty and Fowler, 1994a,b) and northern (Beukers and Jones, 1997) Great Barrier Reef (GBR). The former studies reported density-independent post-settlement mortality, while the latter found density dependent mortality. A key difference between these two cases is that the initial density of recruits was much lower on southern than on northern GBR sites. Hence density dependence was observed at high recruit densities only. Sale (pers. comm.) suggests that in most cases on coral reefs, post-settlement mortality of fish recruits is density independent until numbers get extremely large. This is the form of response adopted in the CORSET.

Predation is frequently implicated as a major source of density dependent mortality in coral reef fish recruits (Hixon, 1991; Carr and Hixon, 1995; Forrester, 1995; Hixon and Carr, 1997; Webster, 2002; Anderson et al., 2007). Hixon and Webster's (2002) literature survey also indicates the role of habitat complexity and the synergistic effects of various groups of predators and interference competitors. Predation and competition may be from con-specifics (Stimson, 1990), other reef species (Beukers and Jones, 1997; Hixon and Carr, 1997; Connell, 1998), or some combination of the two (Anderson et al., 2007). Given that predation and competition pressures may vary between species and reef locations, and are most likely a combination of con- and hetero-specific effects, the implementation of density-dependent mortality in CORSET is as a function of recruit density.

Background mortality of fish recruits in CORSET is 0.2 yr^{-1} , as for damselfish recruits studied by Doherty and Fowler (1994a) and Beukers and Jones (1997) (data summarised in Hixon and Webster, 2002). Background mortality for sea urchin recruits is assumed to be the same as fish recruit mortality. Mortality of fish and sea urchin recruits increases by 0.1 yr^{-1} for every additional 500 000 recruits/ km^2 beyond the threshold of 1 000 000 recruits/ km^2 identified in Jones' (1990) study, up to a maximum mortality rate of 0.98 yr^{-1} , i.e. 0.2, 0.3, 0.4, ... , 0.9, 0.98 (complete mortality of 1.0 yr^{-1} is assumed to be unrealistic). Sensitivity of model behaviour to the maximum post-settlement mortality rate for fish and sea urchins (explored in Section 2.2, Chapter 2 for the range $0.9 - 0.99 \text{ yr}^{-1}$) indicates that modelled fish and urchin biomasses tend to be higher when maximum mortality is equal to 0.9 (the maximum post-settlement mortality rate for fish reported by Russ, 1991), but that this parameter does not influence model behaviour under perturbation scenarios.

CORSET assumes that survival of fish recruits is reduced by 70% in reef cells where coral cover is $\leq 5\%$, based on findings from Holbrook et al. (2008) and Feary et al. (2007). Above 5% coral cover fish recruit survival follows the Shepherd (1982) function: $\text{survival} = aC / [1 + (a/b) C^d]$ (see Holbrook et al., 2008), where C is the coral cover in a particular reef cell and a , b and d are fitted parameters. CORSET uses $a = 1$, $b = 1.11$ and $d = 1$ (i.e. saturating survival).

Coral, fish and sea urchin recruits enter modelled cover/stock after 1 year. From Edmunds' (2007) review of studies of juvenile coral growth rates, the mean diameter growth rate for juvenile corals is 1.67 cm/yr , hence the diameter of year old coral recruits is assumed to be 2.18 cm^2 . Biomasses of year old fish recruits were estimated using von Bertalanffy growth equation parameters from FishBase (Froese and Pauly, 2004). From Carpenter (1997), *Diadema antillarum* recruits reach a diameter of 25 – 30 mm in a year. Assuming the diameter of a 1-year old sea urchin recruit is 27.5 mm, and using the allometric equation from Levitan (1988) for *D. antillarum*, which is $\log_{10} \{\text{live weight (g)}\} = 2.99 \times \log_{10} \{\text{size (mm test diameter)}\} - 3.20$, the biomass of a 1-year old sea urchin recruit was estimated as 12.7 g. This biomass is assumed to apply for Indo-Pacific sea urchin species newly recruited to the 1-year age class.

C. Validation data sources

Table C1: Summary of data used in the validation of CORSET for the Meso-American Reef system (Figures 1.7 and 1.8, Chapter 1). Algal cover refers to the sum of macroalgal and macro turf covers, and piscivore biomass refers to the sum of small-to-intermediate and large piscivorous fish biomasses. Details of validation sources are provided as footnotes.

Variable	Subregion	Year	Source(s)	No. sites	Mean	Range
coral cover (%)	I	1990	a	1	23.0	-
		1993	b	2	1.8	1.7-2.0
		1994	b	2	1.6	1.5-1.7
		1995	b	2	2.0	1.4-3.1
		1999	a, c	2	17.5	14.0-21.0
		1999-2000	d	3	3.6	2.3-3.9
		2002	e	1	24.5	-
		2004-2005	f	1	27.4	16.0-34.0
	II	1999	c	6	16.0	10.0-37.0
		1999-2000	d	7	9.1	3.9-14.2
		2002	e	1	20.3	-
		2004-2005	f	1	18.9	8.0-35.7
	III	2000	g	5	17.3	10.2-24.0
		2004-2005	f	1	26.6	13.3-40.2
	IV	1986	h	1	85.0	-
		1993	b	1	14.1	-
		1994	b	2	18.2	17.6-18.9
		1995	b, h	3	16.8	12.0-21.0
		1996	h	2	40.0	20.0-60.0
		1999	g, h	13	18.0	5.0-36.6
		1999-2000	d	1	4.7	-
		2000	g	18	13.0	2.8-27.9
		2002-2003	i	8	34.0	12.0-52.0
		2004-2005	f	7	26.8	2.3-52.0
		2006	h	1	10.0	-
	V	2002	e	1	10.2	-
		2004-2005	f	2	20.2	11.1-32.3
algal cover (%)	I	1933	b	2	33.3	33.1-33.4
		1994	b	2	79.4	79.1-79.6
		1995	b	1	87.6	-
		1997	c	1	87.0	-
		1999	c	1	79.0	60.0-100.0
		1999-2000	d	3	82.0	77.5-84.3
	II	1997	c	1	66.0	-
		1999	c	1	66.0	55.0-100.0
		1999-2000	d	8	56.3	14.1-81.2

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Variable	Subregion	Year	Source(s)	No. sites	Mean	Range
herbivore biomass (g/m ²)	III	2004-2005	f	1	41.2	12.6-56.8
		2004-2005	f	1	0.2	0.1-0.4
	IV	1993	b	1	32.4	-
		1994	b	2	37.6	34.5-40.6
		1995	b	2	32.7	31.6-33.8
		1999	g	22	88.8	65.0-100.0
		2002-2003	i	8	64.0	8.0-100.0
		2004-2005	f	7	34.5	19.4-67.3
		2006	h	1	16.0	14.0-18.0
	V	2004-2005	f	2	45.5	32.8-54.4
	I	1999	d	3	15.3	11.9-20.3
		2004-2005	f, j	3	40.0	30.8-53.7
	II	1998	k	3	24.3	5.0-48.0
		1999	d	21	26.1	10.2-65.0
	III	2004-2005	f	1	20.8	17.0-26.0
piscivore biomass (g/m ²)	IV	2000	g	3	30.3	24.6-39.7
		2004-2005	f	1	15.6	9.0-21.0
	IV	1999	d, g	14	19.9	6.2-34.8
		2000	g	19	18.6	12.9-28.0
	V	2004-2005	f, j	10	9.9	0.0-47.0
		2004-2005	f	2	50.9	5.0-103.0
	I	1999	d	3	9.6	7.8-13.0
		2004-2005	f, j	3	31.3	0.1-100.6
	II	1998	k	3	14.8	4.0-39.0
		1999	d	21	14.9	2.3-90.1
	III	2004-2005	f	1	3.8	3.0-7.0
		2000	g	3	13.9	13.7-14.1
	IV	2004-2005	f	1	10.5	2.0-25.0
		1999	d, g	14	6.4	1.3-24.4
urchin biomass (g/m ²)	IV	2000	g	19	7.8	1.4-17.9
		2004-2005	f, j	10	9.9	0.0-70.8
	V	2004-2005	f	2	22.6	6.0-57.0
	I	2004-2005	j	1	15.0	0.0-30.0
	IV	2004-2005	j	1	10.0	0.0-40.0

Sources: ^(a)Roy (2004), ^(b)UNESCO (1998), ^(c)Steneck and Lang (2003), ^(d)Arias-González (unpublished data), ^(e)Almada-Villela et al. (2002), ^(f)García-Salgado et al. (2006), ^(g)Marks and Lang (2007), ^(h)McField et al. (2008), ⁽ⁱ⁾Brown-Saracino et al. (2007), ^(j)Newman et al. (2006), ⁽ⁱ⁾Arias-González (1998)

Table C2: Summary of data used in the validation of CORSET for the Philippines/South China Sea region (Figure 4.5, Chapter 4). Algal cover refers to the sum of macroalgal and macroturf covers, and fish biomass refers to the biomass of all fish trophic groups (biomass estimates for particular functional groups of fish were not available for this region). Details of validation sources are provided as footnotes.

Variable	Subregion	Year	Source(s)	No. values reported	Mean	Range
coral cover (%)	I	1988	a	6	32.8	25.6-38.6
		1995	a	9	40.3	16.0-62.0
		1998	b	11	26.6	2.3-53.5
		1999	b	10	14.5	3.5-21.8
		2000	a, b, c, d	77	24.3	4.0-68.7
		2001	a, b, c, d	45	32.3	5.5-47.7
		2002	a, b, c, d	45	32.8	10.7-64.6
		2003	c, d	24	24.0	22.0-45.7
		2004	c, d	6	30.7	24.0-40.0
		2005	c, d	9	25.9	18.0-40.0
	II	2006	c, d	9	26.9	18.0-42.0
		1993	a	8	29.7	12.9-43.1
		1995	a, b	22	31.1	4.7-62.7
		1997	a	8	32.1	10.5-53.0
	III	2001	a	10	29.1	12.3-52.0
		1995	a, b	4	56.9	41.2-72.4
		1996	a, b, c	31	31.0	11.3-59.2
		1999	a, b, c	6	14.7	2.18-29.1
		2000	a, b, c	26	17.3	8.8-30.4
		2001	a, b	13	42.7	24.6-77.3
		2002	c	12	24.1	14.3-44.0
		2004	c	10	15.2	5.4-24.2
	IV	2001	b	5	19.8	9.2-30.8
		2004	d	1	28.0	-
		2007	d	1	35.0	-
	V	1993	a	1	16.3	-
		1996	a	1	7.9	-
		1997	b	24	16.6	0.4-70.0
		1998	b	12	7.1	1.5-11.4
		1999	b	3	10.6	3.3-14.9
algal cover (%)	I	1998	b	5	10.8	0.2-19.6
		1999	b	8	8.3	4.7-16.7
		2000	a, b, c	49	44.5	3.6-84.3
		2001	a, b, c	34	38.8	10.5-64.6
		2002	a, b, c	35	41.2	9.1-64.8
	II	1993	a	6	2.8	0.0-6.9
	III	1996	b	16	2.1	0.3-8.9
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Variable	Subregion	Year	Source(s)	No. values reported	Mean	Range
	IV	1999	b	4	28.4	3.2-54.2
		2000	a, b, c	12	19.1	1.7-49.0
		2001	a, b, c, d	9	70.2	55.4-91.5
		2004	d	6	11.7	3.2-25.8
		2001	b, d	5	33.1	7.7-70.8
		2004	d	1	20.0	-
		2007	d	1	8.0	-
	V	1997	b	22	12.8	0.2-42.3
		1998	b	10	16.6	0.1-79.0
		1999	b	3	13.6	2.5-30.1
fish biomass (g/m ²)	I	1993	e	4	2.2	0.6-4.1
		1995	a, d, e	9	20.9	0.3-112.0
		1996	d, e	36	1.4	0.4-6.7
		1997	a, d, e	21	1.2	0.4-4.0
		1998	a, d, e	26	2.2	0.6-6.5
		2000	a, c, d, e	45	15.0	1.2-137.6
		2001	a, c, d, e	45	7.2	0.7-23.6
		2002	a, c, d, e	59	6.8	0.8-28
		2003	c, d, e	84	7.6	0.9-54.9
		2004	d, e	18	8.9	1.9-24.0
		2005	d, e	43	14.4	1.9-60.0
		2006	d, e	50	16.8	2.6-66.4
		2007	e	34	14.9	3.6-46.4
	II	1991	a	5	27.0	3.3-51.0
		1992	a	6	13.1	1.5-34.2
		1993	a	6	8.9	2.1-14.4
		2002	e	10	42.3	20.8-79.1
		2004	e	10	42.9	13.8-75.6
		2005	e	2	9.3	4.0-14.6
		2006	e	24	45.9	5.7-142.8
		2007	e	12	78.5	25.8-170.8
	III	1996	c	1	10.0	-
		2000	c	1	28.0	-
		2001	e	15	14.6	7.4-29.0
		2002	c	1	25.0	-
		2004	c, e	17	14.1	3.3-26.0
		2006	e	22	25.0	5.7-70.0
		2007	e	29	19.3	6.3-53.0
	IV	2001	d, e	5	12.4	5.8-20.0
		2004	d, e	5	16.0	1.8-22.5
		2007	d, e	5	16.0	3.6-25.0

Sources: ^(a)PhilReefs (2003), ^(b)MIDAS (2004), ^(c)PhilReefs (2005), ^(d)PhilReefs (2008),
^(e)UPMSI-COMECO (unpublished data)

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